THE UNIVERSITY OF EDINBURGH
INSTITUTE OF ATMOSPHERIC AND ENVIRONMENTAL SCIENCES
SCHOOL OF GEOSCIECES

Assessment of carbon sequestration and timber production of Scots pine across Scotland using the process-based model 3-PGN

Georgios Xenakis
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Φιλί μιας καλημέρας

Με μια πνοή σε αγάπησα, με μια ματιά σε βρήκα
και στο φιλί που σου 'δωσα θαρρείς πως βρήκα ελπίδα.
Δεν πίστεψα πως ήσουν εδώ, κι ούτε πιστεύω υπάρχεις
μα σαν τα μάτια ρίξω δίπλα μου θαρρείς πως με ξαφνιάζεις

Γιατί είσαι πνοή που ένιωσα μέσα από τα αναφιλιτά μου
γιατί είσαι το όνειρο που ξύπνησα μέσα απ΄ την καρδιά μου.
Γιατί είσαι αέρας καλοκαιρινός γιορτή μαγιού και αιθέρας
γιατί είσαι εδώ, στοργή, φιλί μιας καλημέρας.

Στην περιπλάνηση μου έλαμψες, τον δρόμο μου φωτίζεις
και σαν λουλούδια άνοιξης θαρρείς πως με στολίζεις.
Κι αν ακόμα δεν κατάλαβα πόσο πολύ μου λείπεις
είναι γιατί πάντα το ήξερα κοντά μου θα γυρίσεις

Γιατί είσαι χτύπος της καρδιάς, ρυθμός μες την ζωή μου
γιατί είσαι ένα τραγούδι όμορφο που βγάζει η φωνή μου.
Είσαι αέρας καλοκαιρινός, γιορτή μαγιού και αιθέρας
Πόσο πολύ σε αγαπώ, φιλί μιας καλημέρας.

Ένα ποίημα και μια ζωή αφιερωμένα σε ένα πρόσωπο φεγγάρι,
σε ένα χαμόγελο ζεστό, σε ένα πρωινό φιλί
... Στην Σοφία μου

A poem and a life dedicated to a face bright as the moon,
to a warm smile, to a morning kiss
...To my Sofia

Abstract

Forests are a valuable resource for humans providing a range of products and services such as construction timber, paper and fuel wood, recreation, as well as living quarters for indigenous populations and habitats for many animal and bird species. Most recent international political agreements such as the Kyoto Protocol emphasise the role of forests as a major sink for atmospheric carbon dioxide mitigation. However, forest areas are rapidly decreasing world wide. Thus, it is vital that efficient strategies and tools are developed to encourage sustainable ecosystem management. These tools must be based on known ecological principles (such as tree physiological and soil nutrient cycle processes), capable of supplying fast and accurate temporal and spatial predictions of the effects of management on both timber production and carbon sequestration.

This thesis had two main objectives. The first was to investigate the environmental factors affecting growth and carbon sequestration of Scots pine (*Pinus sylvestris* L.) across Scotland, by developing a knowledge base through a statistical analysis of old and novel field datasets.

Furthermore, the process-based ecosystem model 3-PGN was developed, by coupling the existing models 3-PG and ICBM. 3-PGN calibrated using a Bayesian approach based on Monte Carlo Markov Chain simulations and it was validated for plantation stands. Sensitivity and uncertainty analyses provided an understanding of the internal feedbacks of the model.

Further simulations gave a detailed eco-physiological interpretation of the environmental factors affecting Scots pine growth and it provided an assessment of carbon sequestration under the scenario of sustainable, normal production and its effects from the environment. Finally, the study investigated the spatial and temporal patterns of timber production and carbon sequestration by using the spatial version of the model and applying advanced spatial analyses techniques.

The second objective was to help close the gap between environmental research and forest management, by setting a strategic framework for a process-based tool for sustainable ecosystem management. The thesis demonstrated the procedures for a site classification scheme based on modelling results and a yield table validation procedure, which can provide a way forward in supporting policies for forest management and ensuring their continued existence in the face of the present and future challenges.

Declaration

I declare that this thesis was composed by myself and that the work contained therein is my own, except where explicitly stated otherwise in the text.

Georgios Xenakis

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This thesis is only a simple summary of all my intellectual growing over the last few years, which I developed through many discussions with people who contributed significantly, either with their knowledge, experience or friendship. This is my only opportunity to thank those who were an influence and a moral support on some of the most exciting and sometimes difficult days of my life.

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Preface

"It is the task of yield studies to examine the quantitative extent of growth processes in the forest in relation to time, site and the economical and technical measures available to man".

Ernest Assman 1961, p.1
In *"The principles of forest yield study"*

"Scotland's trees, woodlands and forests are a central part of our culture, environment and economy. People are benefiting widely from them, actively engaging with and looking after the resource for the use and enjoyment of generations to come".

Vision statement , Forestry Strategy, 2006, p.3
Scottish Executive

"The net changes in greenhouse gas emissions by sources and removals by sinks resulting from direct human-induced land-use change and forestry activities, limited to afforestation, reforestation and deforestation since 1990, measured as verifiable changes in carbon stocks in each commitment period, shall be used to meet the commitments under this Article of each Party included in Annex I. The greenhouse gas emissions by sources and removals by sinks associated with those activities shall be reported in a transparent and verifiable manner and reviewed in accordance with Articles 7 and 8".

Article 3.3, Kyoto Protocol, 1997, p.3

"Trees are not only often profitable as a crop; they are also in the highest degree ornamental, and possess an aesthetic influence of inestimable value. For what objects in nature are so grand and so effective as old trees, with their massive stems and spreading limbs, and their leafy crowns covered with foliage of different shapes and shades? Many hillsides would be comparatively monotonous in appearance but for the plantations of trees of various shades formed upon them. And what would be the effect of the waterfall or the river without trees in their neighbourhood? A country without trees is uninteresting as compared with landscapes in which trees are visible. ... ... But trees are not merely to be admired on account of their beauty and their utility. They inspire a feeling of awe and respect, when we behold the gigantic stems that have stood the storms and stress of four hundred or five hundred years, and often longer, during which many generations of men have come and gone, year by year, and in the fullness and strength of their natural vigour".

James Brown LL.D., 1894, p.15-16
In *"The Forester"*

These four quotes for the world's past, current and future forest management were the motivation of this thesis. The first quote by the German forester Ernst Assman illustrates what forest management has always been depending upon, that is, a sufficient knowledge of forest growth processes and the effects of time and site conditions on timber production, with a target to maximise the economic return from their exploitation. Nowadays, their contribution to earth's climate and environment is not doubted any more. But since the time *Homo sapience* came into being, forest exploitation has had a unique role in the development of the human race: to provide a good source of

construction timber, paper or fuel wood. Forest mensuration emerged as a result of past heavy exploitation when humans realised that forest resources were vital for their existence. This then led into planning and thinking into the future. The sustainability of forests depends on a well established knowledge base on potential growth dynamics.

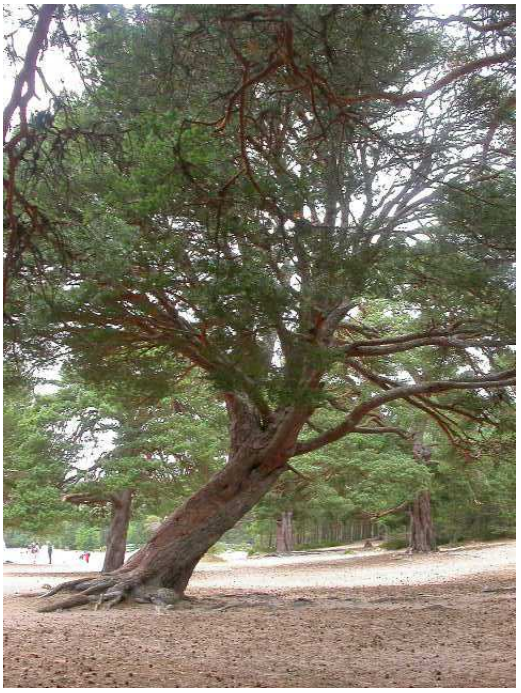

Figure 1: Old Scots pine (*Pinus sylvestris* L.) tree at Glen More forest park.

After thousands of years and at the dawn of the 21st century, forest roles have changed significantly. The old mentality that forests existed purely for human purposes was transformed by a new sense of responsibility in conserving forests. The vision statement by the recently revised Scottish Forestry Strategy illustrates this new mentality, which clearly sees forests not only as a source of timber and shelter but as a unique component in human culture, what is also known as nature. Anthropocentric forest management has now been replaced with a more ecologically based management, after the obvious reduction in global forest expansion. Multi-purpose management objectives include the conservation of forests for new and old indigenous civilizations, provision of habitats for animal and bird populations, provision of recreation activities for the stressful urbanised people, and the maintenance of the forests' contribution to

the earth's biogeochemical and climatic stability.

Figure 2: Beech (*Fagus sylvatica* Cz.) forest at Numfaio, Greece.

The latest realisation arising from climate change has been the role of forests as significant regulators of the earth's climate and as a sink for the human-driven air pollution. The third quote from the Kyoto Protocol (adopted by 164 nations since 1997),

Figure 3: *"A Wheatfield with Cypresses"*. Painting by Vincent Van Gogh. Picture from the National Gallery of Scotland web site (http://www.natgalscot.ac.uk/).

illustrates the potential for current forest policies that attempt to manage forests to maximise their CO_2 sequestration. Their increased photosynthetic potential due to elevated CO_2 concentrations in the atmosphere and N deposition raises the possibility of

changing their management into a tool for atmospheric carbon mitigation.

However, in the modern world of technology, fast-living, large city complexes, modern commodities, national and international politics, humans have forgotten forests and their highly important purpose. Beauty. The words of a forester during the late 19^{th} century could not have described it better. Nature has inspired Antonio Vivaldi to create his ”Four Seasons” masterpiece. Trees and forests have inspired Vincent Van Gogh to create his painting ”A Wheatfield with Cypresses”. Leonardo Da Vinci who said:

> *”The gaps made by air within the bodies of trees and the gaps made by trees within the air will not be shown to the eye over a long distance, because where the whole is perceived with effort, the parts are distinguished with difficulty. Rather a confused mixture is made, which mostly takes on the appearance of the part having the greater bulk”.*

was inspired by trees. He believed that, more so than any other natural phenomenon, trees illustrated the principles of life and growth in nature. His studies on plant growth

Figure 4: *”Star of Bethlehem”*. Drawing by Leonardo Da Vinci. Picture from the British Museum web site (http://www.thebritishmuseum.ac.uk).

flourished through an admiration of nature and a desire to understand its laws.

His ”Study of the Star of Bethlehem” gave the first understanding of botanical func-

tions while his study on water transport in trees produced a universally accepted and still cited rule for branching. Many more poets, composers, painters, sculptors and scientists have been inspired by the imposing existence of forests and trees. They are an integral part of the scenery that most of the time we just take for granted. Human selfishness and the will to conquer nature and other humans, have made us blind to the beauty of nature and detached us from what is our natural home.

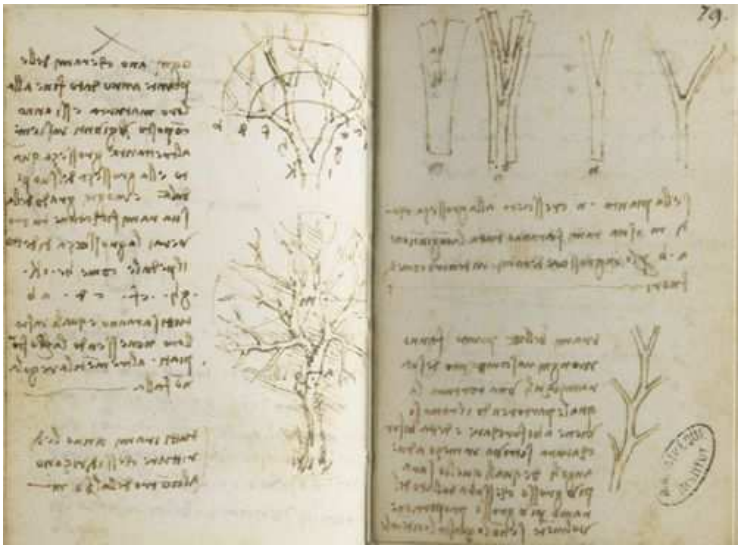

Figure 5: Leonardo Da Vinci's notebook on tree branching and water transport in trees. Picture from the British Museum web site (http://www.thebritishmuseum.ac.uk).

But it is our obligation as managers of forests to respect nature, to implement in the best possible way those policies whose intention is to bring back the lost connection between human and nature. It is an obligation to our future existence, to sustain and protect trees, those standing story-tellers of the earth's history, as they are the ones who can provide a knowledge of the past, while the understanding of their magnificent journey through time can provide the necessary knowledge for the future of human race.

CHAPTER 1

Learning from the past, looking into the future: A general introduction into the world of forest science and management

1.1 Introduction

Forests are one of the most important natural resources on earth. Their unique role as the most important oxygen suppliers on land gives them a vital role in the global ecosystem that humans live in. Their several uses include provision of constructional timber, recreation, paper or fuel wood, while also providing habitat for indigenous populations and many animal and bird species. They extend over 3.952 trillion hectares and they cover 30.3% of the earth's surface. Of that extent, 25.3% is within the European continent, 17.9% in North and Central America, 16.1% in Africa and 14.5% in Asia (FAO Forest Resources Assessment, 2006). 84.4% are under public ownership, 13.3% is under private ownership while 2.4% is under other types of ownerships. However, defforestation due to land-use change, bad management practices and illegal logging have reduced their extent since 1990 from around 4 trillion to 3.952 trillion hectars. Between 1990 and 2000 the rate of decrease of forest area was 0.2%, that is approximately 8.8 billion hectares, while between 2000 and 2005 the decrease has also been 0.2%, that is 7.3 billion hectares. Furthermore, 34.1% of globe's forests are used for timber production, 9.3% for protection from soil erosion, 11.2% for conservation and 3.7% for social services. However, their increased multipurpose role is illustrated by the fact that almost one third of forests is used for multipurpose forestry (33.8%).

Nevertheless, wood production remains the main objective of forests management with 1.7 trillion m^3 over bark used for industrial roundwood and 1.2 trillion m^3 for wood fuel. Wood removal acounted to 3.045 trillion m^3 in 1990 , 2.923 trillion m^3 in 2000 and 3.012 trillion m^3 in 2005 (FAO Forest Resources Assessment, 2006).

These essential roles of forest have reinforced the political will emerged from the observation of increasing air temperatures (Huang *et al*., 2000), caused by anthropogenic and natural gas emissions contributing to the greenhouse effect, urbanization and land-use change (Kalnay and Cai, 2003), resulting into a change in the earth's climate (Moore *et al*., 2002), which also has a great impact on the ecology of many ecosystems, not only in terms of carbon accumulation (Cao and Woodward, 1998) but also with an effect on ecosystem hierarchies in species and vegetation community levels (Walther *et al*., 2002) and soil carbon accumulation and decomposition (Davidson and Janssens, 2006). These are the undesirable consequence that the Kyoto protocol (UNFCCC, 1997) tries to mitigate, by redefining the role of forests in the global carbon cycle and turning them into a tool for reducing national emissions.

All of the above leads to the conclusion that it is vital to develop tools for efficient and sustainable ecosystem management, to provide predictions of future potential growth and the effects of management decisions in all aspects of forests' multi-purpose use. Such goal could be reached by developing tools that are based on tree physiological and soil decomposition principles, providing accurate and fast predictions of temporal and spatial predictions of timber production and carbon sequestration potentials.

1.2 Aim and objectives of the study

The aim of this thesis is to introduce physiologically based models into forest management under a spatial framework and to provide a flexible forest production classification scheme adaptable to modern forest management needs and future climate changes. Furthermore, it aims to provide a better understanding of the major climatic limitations of Scots pine growth and its variability across Scotland, using both an empirical and a process-based methodology. More specific objectives have been set for each of the

chapters, including:

1. To develop a knowledge base of Scots pine growth in Scotland based on empirical regression models with topographic, climatic and soil parameters (Chapter 3).

2. To improve the simplified process-based model 3-PG by introducing an equally simple soil decomposition sub-model ICBM/2N (Chapter 4).

3. To calibrate and validate the new model for Scots pine stands across Scotland, to develop a parameter set applicable across sites and to explore the uncertainty of the parameter set (Chapter 4).

4. To investigate the internal feedbacks between the two process-based models (i.e., 3-PG and ICBM/2N, Chapter 4) .

5. To explore the temporal changes in the spatial patterns of productivity, to provide a thorough investigation into the physiological principles of Scots pine growth and compare it with the already existing knowledge base from the empirical model (Chapter 5).

6. Using advanced spatial analysis technique, to provide an understanding of which environmental factor is responsible for the produced spatial and temporal patterns (Chapter 5).

7. To investigate the effect of current normal yield management on carbon sequestration (Chapter 6).

8. To provide information relevant to answering a most basic question of today's forest management, i.e., which is the best management option, timber or carbon sequestration, for Scots pine stands in Scotland (Chapter 6).

9. To demonstrate a new site classification based on process-based model outputs (Chapters 5 and 6).

1.3 The study species

Scots pine (*Pinus sylvestris* L.) is native to Scotland. It is the most extensively distributed pine species in Europe (Vidakovic, 1991), occurring from Scandinavia, through the whole of central Europe, down to the Pyrenees. Native stands in northern Europe occur in Scotland, Germany, Switzerland, Austria, Czech republic, Slovakia, Poland, Estonia, Lithuania, Latvia, Belarus, Russia and in Finland, Sweden and Norway. In

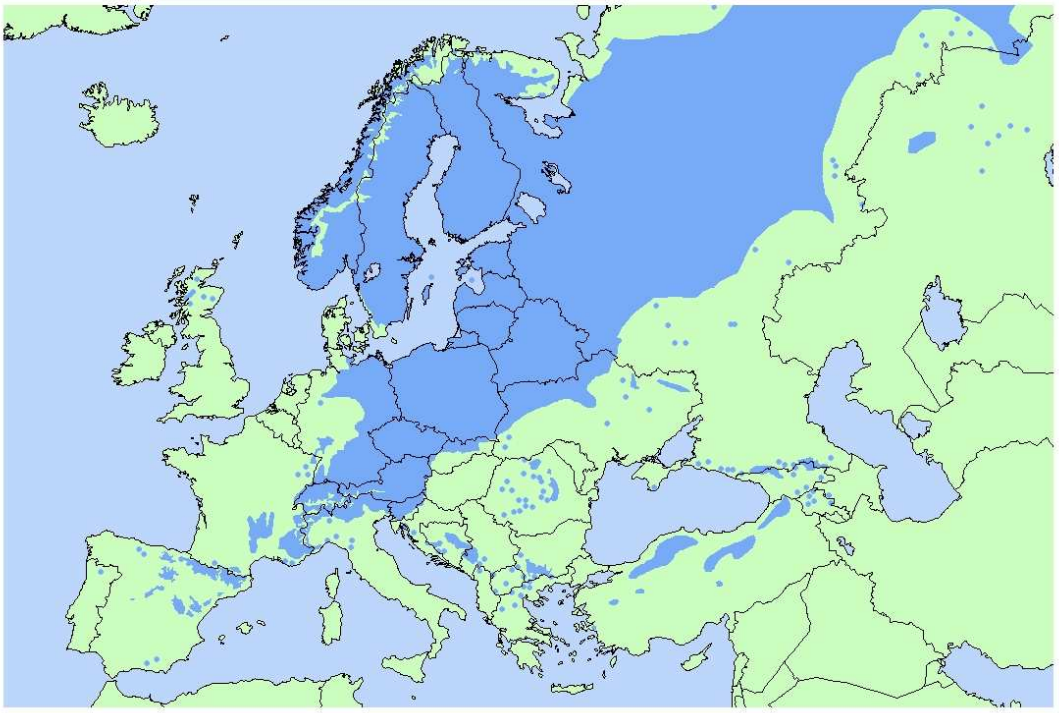

Figure 1.1: Scots pine distribution map in Europe as was compiled by members of the EUFORGEN Conifers Network (Mátyás *et al*., 2004)

southern Europe, it can been found occasionally in Croatia, Bosnia and Serbia, northern Greece (Rodopes mountains) and northern Turkey, northern Italy, northern France and north-east Spain (Figure 1.1).

The southern latitudinal border is $38°41'$ N while the northern border is $70°20'$ N (Vidakovic, 1991, see also Figure 1.1). Scots pine occurs across Great Britain in many commercial plantations (Figure 1.2). In Scotland it occurs from $54°54'$ N to $58°27'$ N, whereas native pinewoods can be found from around $54°$ N to around $57°$ N.

Figure 1.2: An example of Scots pine plantation, approximately 50 years of age (Cardona forest, Scotland).

The trunk normally is straight or slightly bent, while the crown has a shape varying from conical to broadly pyramidal or umbrella-like. Its bark at the base is furrowed with a grey-brown colour while in the upper parts it is reddish-brown and it peels off in thin scales. The leafs are in a fascicle of two, approximately 4-7 cm long bluish-green or grey-green with approximately 2-4 years of life. The flowers appear during May and June, and the seed is ovate, dark brown or grey, 3-5 mm long with the 1,000 seed weight being about 4-8 g. Shoots are grey-brown, whereas buds have an oblong-ovate shape, 6-12 mm long, with a reddish-brown colour and are normally not resinous (Vidakovic, 1991).

It is a pioneer species with a rapid grow in height within the first 50 years of its life, reaching up to 30-40 m. As a pioneer species, it colonises sites after a fire event or after disturbance. The seeds usually germinate on mineral soil and the seedlings are very shade intolerant. Photosynthesis occurs from March through October and trees typically develops a tap root, although it is very adaptable and a shallow root system may be found on some sites, when necessary (Mason *et al.*, 2004).

Scots pine extend between three main climatic zones in Scotland, according to the British Ecological Site Classification (Pyatt *et al*., 2001), i.e. cool moist, cool wet and warm moist. Soil types vary from sandy with a deep water table to deep peats (Pyatt *et al*., 2001), although they typically grow on podzols and ironpans. They can also grow on gleys, brown earths and peats, although their growth on peats is not as good as on more mineral soils. Ground vegetation includes mosses, bracken (*Pteridium aquilinum* (L.) Kuhn), wavy hair-grass (*Deschampsia flexuosa* L.), male fern (*Dryopteris filix-mas* (L.) Schott), wood-sorrel (*Oxalis acetosella* L.), heather (*Calluna vulgaris* (L.) Hull.) and billberry (*Vaccinium myrtillus* L.).

1.4 Forest ecosystem production

Mean annual increment (MAI, $\mathrm{m^3\ ha^{-1}\ yr^{-1}}$), current annual increment (CAI, $\mathrm{m^3\ ha^{-1}}$) and standing volume stocks (V, $\mathrm{m^3\ ha^{-1}}$) are typically the variables employed to qualify forest production. MAI is defined as the average rate of volume increment of a stand from the time of establishment until the present day, whereas CAI is defined as the volume increment of a stand in one year. It is common practise that forest sustainability is ensured in terms of timber production. However, Monserud (2003) supports the view that sustainability should be insured not only for commercial timber production but for ecosystem production as a whole. He recommended using estimates of gross primary production, net primary production and net ecosystem production.

Gross primary production (or gross photosynthetic production, thereafter P_G) is defined as the total $\mathrm{CO_2}$ assimilated by a forest ecosystem through the process of photosynthesis. On the other hand, net primary production (P_N) is the fraction of P_G remaining after autotrophic respiration losses. These losses include photorespiration, maintenance respiration and growth respiration. When heterotrophic respiration (losses of carbon by animal and microbes) is accounted for, what remains is net ecosystem production (P_E) (Waring and Running, 2001). A more precise definition of net ecosystem production sets P_E as the rate at which carbon is accumulated within an ecosystem, that is, carbon stored over a fixed time interval (Randerson *et al*., 2002). According

to this definition, net ecosystem production is estimated by subtracting all outfluxes of carbon (such as those due to fire, leaching, erosion, harvest, herbivores and many other sources) from P_G.

Measuring P_G is a process relatively difficult, because of scaling problems with flux sample measurements and because most of the times allocation to belowground tree compartments is unknown (Ryan, 1991). Empirical relationships exist linking litterfall, maintenance respiration and tissue nitrogen content with belowground carbon allocation (Ryan, 1991). Those relationships allow the estimation of P_G provided that measurements of aboveground carbon allocation exits. Despite these limitations in data availability many modelling exercises have predicted patterns of gross primary production (McMurtrie *et al*., 1990; Berninger, 1997; Williams *et al*., 1997; Bergh *et al*., 1998; Williams *et al*., 2001; Knorr and Heimann, 2001; Grant, 2004), with most of the models utilising the well established model of photosynthesis by Farquhar *et al*. (1982). Most of the mechanistic models simulate P_G at the tree or the canopy levels use time steps of hours. However, accurate upscaling of leaf level photosynthetic production in terrestrial ecosystems is also difficult (Williams *et al*., 1997). The authors argue that up-scaling P_G predictions from leaf to globe is a difficult process using the detailed mechanistic models that currently exist. They also argue that at large spatial scales models predicting P_G should be either simplified or work with larger time steps (days or months).

Given the mensurational and modelling difficulties outlined above for P_G, alternative approaches to characterise forest ecosystem production have been sought, based on estimations of either P_N or P_E. Many methodologies exist for estimating net primary production from field measurements of above or belowground biomass (Ovington, 1957; Albrektson, 1980; Vanninen *et al*., 1996; Oleksyn *et al*., 1999, 2000; Vucetich *et al*., 2000; Gower *et al*., 2001; Xiao *et al*., 2003, 2004; Zianis and Mencuccini, 2005), or from inventory data using biomass expansion factors (Brown *et al*., 1999; Lehtonen *et al*., 2004; Levy *et al*., 2004; Lehtonen, 2005), but with the latter approach frequently criticised as allocation to fine roots growth, mycorrhizae and phytoshpere leaching are not considered. The finding that the ratio between gross and net ecosystem production

could be considered constant across biomes (Waring *et al*., 1998) was regarded as a major step forward in P_G estimation as it would allow making use of field measurements of P_N (after accounting for the losses mentioned above) to estimate P_G. This constant ratio is now used in many modelling exercises (Landsberg and Waring, 1997; Sands *et al*., 2000), despite doubts raised recently on the universality of its value (Mäkelä and Valentine, 2001).

Net primary production is normally estimated using eddy covariance measurements (Running, 1994; Kellomäki and Wang, 2000; Markkanen *et al*., 2001; Wirth *et al*., 2002; Baldocchi, 2003; Kolari *et al*., 2004; Wang *et al*., 2004a,b). Eddy covariance measures the upward and downward movements of air and the concentration of carbon dioxide ($[\mathrm{CO}_2\ ]$) moved by this turbulent motions to determine the net difference across the canopy-atmosphere interface (Baldocchi, 2003). A statistical analysis of those fluxes provides estimates of net ecosystem exchange or net ecosystem production. Eddy covariance measurements can provide the calibration data for many ecosystem models (Running and Gower, 1991; Wang *et al*., 2004a,b), which can be used to explain many of the eco-physiological processes of forest production.

Other data-driven methodologies include the utilisation of remote sensing data at the regional (Jiang *et al*., 1999; Mickler *et al*., 2002a; Hörsch, 2003; Zheng *et al*., 2004) or global scale (Field *et al*., 1995; Prince and Goward, 1995), or alternatively modelling approaches at the stand (Waring, 2000; Grant, 2004; Landsberg *et al*., 2005; Bugg *et al*., 2006), regional (Coops and Waring, 2001; Coops *et al*., 2001b; Tickle *et al*., 2001a,b; Mickler *et al*., 2002a,b; Zuo *et al*., 2003; Swenson *et al*., 2005) or global scale (Foley, 1994; Cao *et al*., 1996), modelling approaches based on remote sensing data at the regional (Coops *et al*., 1998; Coops and Waring, 2001; Coops *et al*., 2001b; Swenson *et al*., 2005) and global scale (Liu *et al*., 1997) and modelling approaches utilising spatial interpolated data under a Geographical Information System (GIS) framework (Cannell and Milne, 1995; Ditzer *et al*., 2000; Kimball *et al*., 2000; Tickle *et al*., 2001a,b; Williams *et al*., 2001; Tan and Shibasaki, 2003; Zuo *et al*., 2003; Seidl *et al*., 2005; Swenson *et al*., 2005; Bugg *et al*., 2006).

Reviewing productivity of forest ecosystems in general is vital to a better understanding

of productivity dynamics. For that reason, many studies have provided global estimates of terrestrial P_G or P_N (Foley, 1994; Field *et al*., 1995; Prince and Goward, 1995; Cao *et al*., 1996; Hunt *et al*., 1996; Knorr and Heimann, 2001). Field *et al*. (1995) gave an estimation of global annual terrestrial P_N at 48,000 $\mathrm{M\,tC\,yr^{-1}}$ using the CASA model combined with satellite and surface data. Foley (1994) reported simulations using the DEMETER process-based model and found that P_N globally was 61,200 $\mathrm{M\,tC\,yr^{-1}}$. Bolin and Fung (1992), (cited by Williams *et al*. (1997)) gave a prediction for terrestrial plants of 90,000 $\mathrm{M\,tC\,yr^{-1}}$ for P_N and 130,000 $\mathrm{M\,tC\,yr^{-1}}$ of P_G, while Hunt *et al*. (1996) estimated 52,000 $\mathrm{M\,tC}$ for global P_N and 66,000 $\mathrm{M\,tC}$ for global heterotrophic respiration. On the other hand, Cao *et al*. (1996) gave P_N at 0,45 $\mathrm{tC\,ha^{-1}\,yr^{-1}}$ and 8.20 $\mathrm{tC\,ha^{-1}\,yr^{-1}}$ for northern bogs and tropical swamps respectively, whereas Berthelot *et al*. (2002) gave a value of global P_N of 58,300 $\mathrm{M\,tC\,yr^{-1}}$. Cao and Woodward (1998) used a process-based model and predicted global P_N at 57,000 $\mathrm{M\,tC\,yr^{-1}}$, while they gave carbon stocks for vegetation at 640,000 $\mathrm{M\,tC}$ for vegetation and 1.358 million $\mathrm{M\,tC}$ for soils. They also found that P_E was negative during October with values -500 $\mathrm{M\,tC}$, whereas ecosystem accumulated carbon during July with values up to 1,600 $\mathrm{M\,tC}$. Finally, Knorr and Heimann (2001) using the global vegetation model BETHY found that global P_G was 183,390 $\mathrm{M\,tC\,yr^{-1}}$, while P_N was 75 $\mathrm{M\,tC\,yr^{-1}}$ with a mean of 6.14 $\mathrm{tC\ ha^{-1}\ yr^{-1}}$. Forest carbon stocks world wide are estimated to be 186,360 $\mathrm{M\ tC}$ in aboveground biomass, 51,459 $\mathrm{M\ tC}$ in belowground biomass, 32,705 $\mathrm{M\ tC}$ in dead wood biomass, 13,511 $\mathrm{M\ tC}$ in litter and 229,151 $\mathrm{M\ tC}$ in soil carbon (FAO Forest Resources Assessment, 2006).

The extensive literature review on Scots pine dynamics across Europe provided a level of comparison for the modelled and observed productivity of Scots pine in Scotland. Many studies have investigated forest ecosystem production at a regional or stand scale. Schulze *et al*. (1999) gave values for the Eurosiberian boreal region between 1.23 and 4.19 $\mathrm{tC\ ha^{-1}\ yr^{-1}}$. On the other hand, Gower *et al*. (2001) presented values of Scots pine aboveground P_N for Europe between 16.49 and 86.56 $\mathrm{tC\ ha^{-1}}$, and between 0.678 and 32.15 $\mathrm{tC\ ha^{-1}}$ for belowground. Aboveground P_N of Scots pine in Russia was reported to range from 0.56 $\mathrm{tC\ ha^{-1}\ yr^{-1}}$ to 6.75 $\mathrm{tC\ ha^{-1}\ yr^{-1}}$, whereas belowground P_N was between 0.678 and 32.15 $\mathrm{tC\ ha^{-1}\ yr^{-1}}$ (Gower *et al*., 2001).

Wirth *et al*. (1999) on the other hand, gave an estimation of 6.36 $\mathrm{tC\ ha^{-1}\ yr^{-1}}$ for Siberia. Oleksyn *et al*. (2000) reported aboveground P_N for Scots pine ranging from 19.2 to 50.1 $\mathrm{tCha^{-1}yr^{-1}}$ for north Europe, 40.3 to 72.5 $\mathrm{tCha^{-1}yr^{-1}}$ for central Europe and 9.4 to 17.5 $\mathrm{tC\ ha^{-1}\ yr^{-1}}$ for south Europe. Scots pine ecosystems were reported to have P_N of about 3.02 $\mathrm{tC\ ha^{-1}\ yr^{-1}}$ in Finland and 3.8 $\mathrm{tC\ ha^{-1}\ yr^{-1}}$ in Sweden (Borghetti and Magnani, 2003), while Kolari *et al*. (2004) gave an estimation of about 2.52 $\mathrm{tC\ ha^{-1}\ yr^{-1}}$ for sites in Finland. Gross photosynthetic production of Scots pine in Europe was regarded to vary between 18.83 $\mathrm{tC\ ha^{-1}\ yr^{-1}}$ and 30.79 $\mathrm{tC\ ha^{-1}\ yr^{-1}}$ (Berninger, 1997). In Scots pine stands older than 100 years old, net ecosystem production was reported to be as low as 0.1 $\mathrm{tC\,ha^{-1}\,yr^{-1}}$ in Sweden (Borghetti and Magnani, 2003) and 0.19 $\mathrm{tC\ ha^{-1}\ yr^{-1}}$ in Siberia (Wirth *et al*., 2002). Dolman *et al*. (2002) found that Scots pine in the Netherlands growing on sandy soils gave a P_G of 1.559 $\mathrm{tC\,ha^{-1}\,yr^{-1}}$, whereas annual carbon sequestration was 0.338 $\mathrm{tC\,ha^{-1}}$. Other studies have demonstrated the application of a process-based model for estimating the spatial distribution of net primary production (Mickler *et al*., 2002a,b). Zheng *et al*. (2004) using remote sensing and field data found that Scots pine P_N in Finland and Sweden ranged from 1.72 $\mathrm{tCha^{-1}yr^{-1}}$ to 10.91 $\mathrm{tCha^{-1}yr^{-1}}$ with a mean of 4.08 $\mathrm{tCha^{-1}yr^{-1}}$, whereas Vucetich *et al*. (2000) found that total ecosystem carbon content increased between sites with different latitudes from 0.79 $\mathrm{tC\ ha^{-1}\ yr^{-1}}$ in the south to 1.87 $\mathrm{tC\,ha^{-1}\,yr^{-1}}$ in the northern latitude sites.

Carbon stocks of British vegetation is estimated to be 113,8 million tC, of which almost 80% is in forest and woodland ecosystems (Cannell and Milne, 1995). From the total carbon stored in vegetation, 25.4% is conifer woodlands, 46.8% broadleaved woodlands and 8.5% mixed woodlands. Carbon stocks in Scots pine stands is estimated to be 7.1 tC, that is 7.7% of the total carbon stored in woodlands (Cannell and Milne, 1995). Currently forests in Great Britain appear to sequester 1.5 - 1.7 million $\mathrm{tC\,yr^{-1}}$ in trees, 0.3 - 0.5 $\mathrm{tC\,yr^{-1}}$ in litter and 0.5 million $\mathrm{tC\,yr^{-1}}$ (Cannell and Milne, 1995).

Also important is to understand the response of Scots pine productivity on environmental changes. For that reason, many projects have concentrated on the potential

effects of climate change on forest productivity in terms of P_N and P_G (Kellomäki and Väisänen, 1997; Kellomäki *et al*., 1997; Berthelot *et al*., 2002; Jach *et al*., 2000; Zheng *et al*., 2002). Zheng *et al*. (2002) reported that Norway spruce stands P_G will increase from 26.9 $\mathrm{tDM\,ha^{-1}\,yr^{-1}}$ to 31.8 $\mathrm{tDM\,ha^{-1}\,yr^{-1}}$ with a 4°C increase in temperature, to 33 $\mathrm{tDM\,ha^{-1}\,yr^{-1}}$ with a double $\mathrm{CO_2}$ air concentration and to 33.9 $\mathrm{tDM\,ha^{-1}\,yr^{-1}}$ with both the above scenarios. In the same way P_N was reported to increase from 10.1 $\mathrm{tDM\,ha^{-1}\,yr^{-1}}$, to 10.8 $\mathrm{tDM\,ha^{-1}\,yr^{-1}}$, 13.8 $\mathrm{tDM\,ha^{-1}\,yr^{-1}}$ and 15.3 $\mathrm{tDM\,ha^{-1}\,yr^{-1}}$, respectively for the same scenarios. Kellomäki and Kolstrom (1994) also reported an increase in P_N for northern and southern Finland with increasing temperature and double [$\mathrm{CO_2}$], of 19% and 8% for the first scenario and in the two regions, 21% and 23% for the second scenario and 40% and 32% for the third scenario. Jach *et al*. (2000) also argued that potential increases of [$\mathrm{CO_2}$] will not necessarily increase forest production without a parallel increase in leaf nitrogen concentration. Pussinen *et al*. (2002) supported that warmer climatic conditions combined with increased nitrogen depostion will enhance forest productivity and timber yield resulting in shorter rotations, view that was strongly supported by Cannell *et al*. (1998). Bergh *et al*. (2003) used BIOMASS, a process-based simulation model to investigate the effects of climate change on several tree species and found that net primary production could increase between 25 - 40% for conifers and beech due to increased photosynthesis. Cao and Woodward (1998) showed that double atmospheric [$\mathrm{CO_2}$] will increse P_E by 76% while it will enhance P_N by 25%. On the other hand, simulations in which climate change occured without the increase in atmospheric [$\mathrm{CO_2}$] showed that P_N and soil carbon stocks were reduced.

From the literature review it is apparent that the majority of the range of methodologies applied for estimating current ecosystem production and future responses to environmental factors lack of any the possibility to estimate variables meaningful to forest managers. It is thus crucial the development of a simple ecosystem tool, capable to introduce basic eco-physiological principles into forest production estimation, allowing flexibility in scenario modelling based on management decision and future climate change but also with the possibility of producing variables useful to foresters.

1.5 Soil carbon stocks and fluxes

Soils are fundamental components of an ecosystem production. Soils contain almost half of the world's carbon stored in a forest (FAO Forest Resources Assessment, 2006). As climate changes, changes in decomposition caused by increasing temperatures may increase losses of carbon (Davidson and Janssens, 2006), with higher rates of loss for soils with higher carbon contents (Bellamy *et al*., 2005), reducing the potential forest ecosystem production. Although much research is concentrated on exploring the effect of climate change on whole ecosystem production (Kellomäki *et al*., 1997; Jach *et al*., 2000; Berthelot *et al*., 2002; Zheng *et al*., 2002), fewer studies have explored the effects of increasing temperatures (Bellamy *et al*., 2005; Davidson and Janssens, 2006), forest management practices (Zerva, 2005; Zerva *et al*., 2005), afforestation (Paul *et al*., 2002, 2003b), increased harvested biomass combined with increased temperature (Ågren, 2003), land-use change (Oliver *et al*., 2004) or of stand age on soil carbon stocks and organic mater decomposition (Peltoniemi *et al*., 2004; Zerva *et al*., 2005). Although many well established models of carbon decomposition exist, like CENTURY (Moorhead, 1991; Kelly *et al*., 1997; Kirschbaum and Paul, 2002), RothC (Jenkinson, 1990) and new models like YASSO (Liski *et al*., 2005) and ICBM (Andrén and Kätterer, 1997; Kätterer and Andrén, 2001), only a few of these are integrated into a complete ecosystem process-based framework, where ecosystem production is predicted on basic principles of tree physiology, growth, mortality and soil organic matter decomposition (Thornley, 1991; Peng *et al*., 2002; Corbeels *et al*., 2005a,b).

Global predictions of soil carbon stocks are approximately 229,151 $\mathrm{M\ tC}$ for forested areas and 2,496 $\mathrm{M\ tC}$ for other wooded areas (FAO Forest Resources Assessment, 2006). Wetlands, peatlands and permafrost soils have higher carbon densities than upland mineral soils (Davidson and Janssens, 2006) with peatlands down to 3m depth having approximately 400,000 - 500,000 $\mathrm{M\ tC}$ and permafrost soils having 400,000 $\mathrm{M\ tC}$ for the same depth. However, these soils appear to have greater potential for losses due to global warning, i.e., up to 100,000 $\mathrm{M\ tC}$. This supports the results by Bellamy *et al*. (2005) who found that UK soils with carbon content greater than 100

gkg^{-1} had a loss of carbon more than 2% a year, whereas the mean rate of loss fro soils with lower carbon content was 0.6% a year.

Zerva *et al*. (2005) investigated soil carbon stocks and fluxes in a chronosequence of Sitka spruce stands in Northern England. They found that carbon stocks for 40 year old stand were approximately 140 $\mathrm{tC\ ha^{-1}}$, which was lower than in the surrounding unplanted grasslands (274 $\mathrm{tC\ ha^{-1}}$). They also investigated the effects of the progression from first to second rotation carbon stocks and found that soil carbon accumulated during the second rotation from 147 $\mathrm{tC\ ha^{-1}}$ at age 12, to 181 $\mathrm{tC\ ha^{-1}}$ at age 20 and finally at 249 $\mathrm{tC\ ha^{-1}}$ at the age 30. Clearfelling sites appeared to enhance soil respiration by approximately 5.6 $\mathrm{tC\ ha^{-1}}$, turning soils from a sink to a source of both CO_2 and methane (Zerva and Mencuccini, 2005). Soil stocks in Scots pine stands are normally lower, with values between 50 and 90 $\mathrm{tC\ ha^{-1}}$ in Finland (Hyvönen *et al*., 2002). Similar values for Scots pine stands were found by Wilson and Puri (2001) for the first 30 cm of soil (i.e., approximately 121.5 $\mathrm{tC\,ha^{-1}}$) whereas values for moorland were higher (147.47 $\mathrm{tC\ ha^{-1}}$) and similar to Garnett *et al*. (2001) predictions of 130 $\mathrm{tC\ ha^{-1}}$. Interestingly, soil carbon stocks were estimated to be 214.8 $\mathrm{tC\ ha^{-1}}$ down to 79 cm depth. Peltoniemi *et al*. (2004) carried out a modelling exercise using the YASSO model and predicted soil carbon stocks to be approximately 68 to 70 $\mathrm{tC\ ha^{-1}}$ under Scots pine forests, while stocks in the organic layer increased by an average of 0.047 $\mathrm{tC ha^{-1}\,yr^{-1}}$ with increasing stand age. They also found that stocks declined to a minimum 20 years after clear felling whereas the subsequent increase was on average 0.058 $\mathrm{tC\ ha^{-1}\ yr^{-1}}$.

Liski *et al*. (2002) investigated the changes in soil carbon stocks in western Europe and found there is a significant increase over time. More specifically, they found that in 1990 the soil carbon sink amounted accounted to almost 32% of the tree carbon sink and that by 2040 the soil carbon sink will increase from 26 $\mathrm{M\ tC\ yr^{-1}}$ to 43 $\mathrm{M\ tC\ yr^{-1}}$. This increase was predicted to be due to increasing litter fall as European forests became older. On the other hand, Ågren (2003) supported the view that the removal of all thinning material in Swedish forests such as needles, branches and tops (otherwise left during harvesting operations) will cause a decrease in soil carbon stocks

of 0.4 $\mathrm{M\,tC\,yr^{-1}}$, that is 59 $\mathrm{M\,tC}$ after 150 years. They also predicted that an increase in temperature due to climate change will increase carbon losses by 0.9 $\mathrm{M\,tC\,yr^{-1}}$, which was partially counterbalanced by the increases in production, leaving a net loss of carbon of up ot 0.5 $\mathrm{M\,tC\,yr^{-1}}$.

Finally, Oliver *et al*. (2004) found a significant decrease in soil carbon stocks with land-use change from pastures to forest from 20.3 $\mathrm{tC\,ha^{-1}}$ to 19.6 and 8.5 $\mathrm{tC\,ha^{-1}}$ at two different sites respectively, suggesting that land use change from pasture to soils increase soil respiration as also observed after clear felling (Zerva and Mencuccini, 2005).

Current research on the modelling of soil organic matter decomposition has mostly concentrated on predicting heterotrophic respiration as a consequence of climate change, without however introducing soil organic matter decomposition in a complete ecosystem management scheme, where decisions for sustainability are also based on soil decomposition dynamics. The development of a management tool using the knowledge of soil carbon decomposition will ensure the possibility of estimating potential effects of human activities and future climate change on soil nutrient status and thus on potential forest ecosystem productivity can be estimated.

1.6 Modelling forest production

According to Thornley and Johnson (1990), models are mathematical expressions providing a quantitative description and understanding of plant mechanisms. Ågren and Bosatta (1996) shaped a different view of what is an ecological model. They support that:

> *"A theory is a set of concepts (the language) linked by mathematics (the tool) and used to analyse specific problems by being translated through models".*

Peng (2000) supported that models are useful to predict changes of biological ecosystems in order to obtain necessary information for decision making, where Johnsen *et*

al. (2001) supported that mathematical representations incorporate our understanding of physiological or ecological mechanisms into algorithms.

But models are nothing more than a representation of the knowledge we have on the natural processes of plant growth or reaching a good decision according to current needs.

According to Assman (1961), yield studies have the target of providing sufficient knowledge of current and future forest growth to support economical decisions. Modelling of forest production has always been the objective of yield studies. Here we present a small review of modelling techniques available to forest managers, whilst we provide a discussion of their applicability to current forest policies.

1.6.1 Growth models

Growth yield models were the first consistent attempt introduced by foresters into modelling current and future forest growth dynamics with the single objective of forecasting timber yields. Yield models were mainly developed by German foresters during the 18^{th} century, however they were not completely unknown beforehand as they appeared in the 17^{th} century in the form of Chinese Lung Ch'uan codes (Vanclay, 1994). Yield models are statistical functions describing tree biological inter-relationships, such as between diameter at breast height and tree height, established by analysing a range of measurements extracted by an extensive network of permanent sample plots. They describe the development of stand or individual tree characteristics, such as basal area and volume with stand age.

Site quality classification (or site index) on the other hand, is one of the major components of forest management, timber based decision making. Because of its direct linkage with timber site productivity, through the growth and yield models, it is considered as one of the most important factor for planning actions and making decisions. Its use is essential on the evaluation of the effects of environmental factors, stand density and structure on tree growth and consequently on timber production. The problem of site

quality was addressed by the German forester Crarl Heyer (1845, as cited by Assman, 1961) who supported that site analysis should be directed towards *"the investigation and gauging of site quality factors"*, with Franz v. Baur (1881, as cited by Assman, 1961) defining mean height of trees as the *"most exact and only accurate guide not only to the evaluation of a reasonably stocked and normally-grown stand but also its quality class*. Thus, site index was developed as the criterion used for site classification and construction of yield tables. Site-quality index is defined as the top height of dominant and co-dominant trees of a stand at a predetermined reference breast-height age. Several ways exist for estimating site index, divided into two main categories. The phytometric, including the height-diameter relationship and the biophysical (or geobiometric), including environmental factors, like climate, topography, soil and vegetation. The most commonly used way of estimating site index is the height-age relationship, which comes after stem analysis of even-aged stands. Its easy assessment makes it also the most accurate way to estimate site index.

Elfving and Kiviste (1997) demonstrated the construction of site index curves for Scots pine in Sweden by evaluating an array of thirteen functions between age and height using a series of permanent sample plot data and by testing three different methodologies, including guide curve method, the parameter prediction method and the difference equation method. Pienaar and Turnbull (1973) investigated the application of a Chapman-Richards generalization of the Von Bertalanffy's growth model for basal area growth providing predictions of basal area development of stands of different initial stocking and subsequent thinning regimes. On the other hand Yang *et al*. (1978) used a custom version of the Weibull-type function to provide estimates of tree volume and height growth in relation to age. Chang (1984) used a logarithmic-reciprocal yield function model, which provided estimates of volume increment and stocks at different stand ages by allowing different initial stocking and site index to account for local differences in productivity. Gatzojannis (2000) developed site index curves for *Abies cephalonica* Loud. in Greece by testing two different methods, one based on an age-height parameter prediction model and the other on a difference equation model. Many studies have recently applied individual-based models to predict growth without the explicit use of site index, including the study by Trasobares *et al*. (2004) who tested

four tree-level distance-independent simulation models for predicting diameter, height, volume growth and survival of *Pinus halepensis* Mill. in North-East Spain. Similarly, Palahi *et al*. (2004) evaluated several height-age models to construct site index models of *Pinus sylvestris* L. in North-East Spain following the proposed methodologies by Elfving and Kiviste (1997) and exploring models such as the Chapman-Richards, Shumacher and Hossfeld equations, whereas Mehtätalo (2005) uses the Chapman-Richards function to fit observations of height-age relation for the same species in Finland.

1.6.1.1 Yield tables

The potential yield production for a specific site quality can be summarised by the construction of yield tables. Yield tables are nothing more than the tabular result of growth simulation models with the scope of showing *"the yield per acre which can be expected from stands of timber at given ages or for given periods, in terms of a given unit of volume or of product"* (Chapman, 1874). The first yield tables were constructed between 1874 and 1880 by German forest institutes and they only showed volume and yield of stands, without any information for the development on other parameters of the stands, such as height, diameter, or even the losses of volume during the period of prediction. These yield tables gave predictions usually for period of five or ten years. Nowadays, new yield tables include additional information beside standing volume and yield, including:

- Mean and top height
- Mean diameter and basal area
- Stand volume and yield
- Intermediate crop volume
- Number of stems
- Total and current increment

Yield tables are used primarily *"to predict the yield of existing stands"* (Chapman, 1874). According to the same source yield tables are the data required for determination of the value of forest land, determination of profits of forestry, damage appraisal of forest property, choice of rotation, advisability of thinning and choice of species.

According to Gatzojannis (1999) on the other hand yield tables are also used for predict the future evolution of the stands, estimate the yield and productivity of the stands, predict-estimate normal stand volume, estimate current increment and plan the sustainable yield.

The first yield tables for Great Britain were constructed after the first world war for several tree species, including Scots pine (*Pinus sylvestris* L.), Norway spruce (*Picea abies* (L.) Karst.) and European larch (*Larix decidua* P. Mill.) (Forestry Commission, 1920), but since then yield tables have been constructed for many other species such as Corsican pine, lodgepole pine, sitka spruce, Norway spruce, Japanese larch, Douglas fir, western hemlock, cedar, cypress, oak, beech, sycamore, ash, birch, and poplar (Hamilton and Christie, 1971), sweet chestnut (Everard and Christie, 1995), grand fir and noble fir (Christie and Lewis, 1961) and northofagus (Christie *et al*., 1974). In today's forest management, the yield tables by Edwards and Christie (1981) after a most recent revision, are used for all major tree species.

1.6.1.2 The problem with yield models

Whilst growth yield models and yield tables give a reliable and easy way of assessing potential and current forest growth dynamics their application has some hidden pitfalls. One question arising from their application is whether *"we can expect stands reaching the same mean heights, or top heights, at a certain age always to have the same total crop yields"* (Assman, 1961). General yield tables provide a general description of future yields of stands regardless of short-term environmental effects across sites. Furthermore, the statistical relationships embedded in the yield tables are valid only for the stands for which data were collected, as their construction is costly due to the requirement of data collection at a large scale. Construction of local yield tables may

be *representative of the region in which they are to be applied"* (Assman, 1961), nevertheless their construction demands further localised data collection.

Moreover the objectives of today's multi-purpose forest management include recreation, soil protection, water quality improvement, forest tourism, protection of cultural heritage and contribution to human health and enjoyment. This range of objectives is thought to be better catered for by a continuous cover forestry scheme. However, yield tables lack information about habitat evolution and regeneration, as their range of application was limited to plantation forestry. They are also incapable of predicting the impact of any human driven activities such as fertilisation, different intensity thinnings or fire, unless specific data are collected for these purposes.

In addition, climate change is bringing about increases in temperature and precipitation, while pollution increasing atmospheric carbon dioxide (CO_2) concentration and is causing nitrogen deposition. Growth yield models with their strict statistical relationships do not allow any inclusion of possible effects on trees and ecosystems as they lack any ecological representation of processes such as photosynthetic capacity and nutrient cycle.

1.6.2 Biophysical site index models

An increased demand for more site-specific estimation of tree growth and yield has been growing over the decades. It is known that site influences the productivity of stands with factors such as temperature, precipitation, aspect, slope, soil nutrient availability, soil depth, etc. This research effort has resulted in the linkage of site classification to those biophysical parameters and consequently to site index estimation, with subsequent development of more advanced growth and yield models.

The many projects that have tried to produce site index models using site classifications based on environmental (or biophysical) factors can be grouped into three main classes. The first method consists in stratifying site index curves as a function of some biophysical variables. This approach tends to produce large, complicated models, where

ecological diversity is large. The second method consists empirically relating some biophysical factors with a phytometric site index, but this method may bring problems if correlation between the phytometric site index and the biophysical variables is weak. The third and final method consists in defining a site index function whose parameters are the biophysical variables. To evaluate these models, a comparison needs to be made with a phytometric estimation, which is one of the problems that this approaches have, given one needs an estimate of the true site index productivity. However, the comparison can show if the estimation is more or less accurate than the one obtained using a phytometric site index approach.

One of the earliest efforts to correlate site index and environmental factors was by Mogren and Dolph (1972), who related the depth of the A horizon, the depth of the C horizon, stoniness and annual precipitation with an index of production. Woollons *et al*. (1997) used solar radiation, annual rainfall, mean temperature, latitude, longitude, altitude, aspect and slope for his site index model. Corona *et al*. (1998) uses temperature, rainfall, elevation, aspect, topographical exposure, water deficit, soil depth and pH to estimate site index for Douglas-fir plantations in central Italy. Klinka and Carter (1990) used climatic and soil characteristics to derive a site index model which was only a function of the soil characteristics (e.g., soil moisture regime). Ung *et al*. (2001) provided estimates of tree height growth based on diameter, but also included additional variables in a multivariate non-linear model, such as degree-days, vapour pressure deficit, precipitation, aridity index and water holding capacity for site index estimation for *Abies balsamea* L. Mill, *Picea mariana* Mill. BSP, *Populus tremuloides* Michx., and *Betula papyrifera* Marsh.

Fontes *et al*. (2003) provided a multiple regression analysis of site index with a variety of soil, topographic and climatic variables from a range of 39 plots across Portugal, including latitude, altitude, aspect, slope, soil depth, soil pH, water holding capacity, total nitrogen, stoniness and soil texture, exchangeable minerals (e.g., K, Na, Mg, Ca etc.), annual mean solar radiation, annual mean temperature, annual total precipitation, moisture deficit and many others. Similarly complex was the biophysical site index model constructed by Bravo and Montero (2001) for Scots pine in northern Spain,

whereas Romanya and Vallejo (2004) produced similar type of biophysical model for *Pinus radiata* D.Don., while also including litterfall rates and many soil biochemical variables, such as C:N ratios, carbon and nitrogen stocks in the organic layers, soil depth, mineral carbon and nitrogen content in the soil, and foliar N, P, K, S and Mg.

Biophysical site index models are applicable not only for prediction of potential height growth but also for the investigation of the effects of climatic and site variables on growth. Fries *et al*. (1998) used a model which related site index with a series of temperature variables, exposure variables and dummy variables to investigate the effects of temperature on site productivity of Scots pine and lodgepole pine in Finland and Sweden, whereas Holmgren (1994) used a biophysical site index model to investigate the combined effects of topographic variables and geochemical effects on site quality for Scots pine and Norway spruce in Sweden. MacFarlane *et al*. (2000) on the other hand developed a site index model including variables such as stand density and investigated the effect of density on height development, whereas Hokka and Ojansuu (2004) used a customised site index model to investigate the effects of soil drainage on height development of Scots pine. Finally, Louw and Scholes (2006) used a Chapman-Richards type model of site index for *Pinus patula* ex Schlecht. & Cham., which was then compared with a biophysical site index model including soil chemical variables such as N, P, K, Ca, Mg, Na soil content, pH, organic carbon content, soil texture and topographic variables and with the process-based model 3-PG.

In Great Britain, height growth for Scots pine was described by a large study across the country (White, 1982a,b), which provided a multilinear regression model with topographic variables such as slope, elevation and grid co-ordinates, competition variables including grazing, thinning type and intensity and height of ground flora, soil variables such as total depth and phosphorus availability, soil physical variables such as silt content, water holding capacity and stoniness, soil chemical variables such as pH, total phosphorus, monoterpene and climatic variables such as temperature, rainfall and wind direction.

It is a common practise for biophysical models to represent growth of the stand in terms of height (Klinka and Carter, 1990; Mogren and Dolph, 1972; Bravo and Mon-

tero, 2001; Ung *et al*., 2001; Fontes *et al*., 2003), however many studies have also investigated the application of biophysical models using other growth variables, such as basal area and volume stocks (Pienaar and Turnbull, 1973; Woollons *et al*., 1997), current annual volume increment (Milner *et al*., 1996) or general yield class (Cook *et al*., 1977; Tyler *et al*., 1996; Bateman and Lovett, 1998). Geographic Information Systems (GIS) have also been a very useful tool in providing biophysical predictions of site production spatially distributed over large areas (Bateman and Lovett, 1998; Mitsuda *et al*., 2001; Korkalainen and Lauren, 2006). Mitsuda *et al*. (2001) demonstrated the application of a biophysical site index model with spatially interpolated independent variables for the multiple regression models, providing accurate predictions of height development, while Korkalainen and Lauren (2006) demonstrated the use of GIS as a data collection tool for a phytogeomorphologic site index model.

1.6.2.1 Non-applicability of biophysical models for forest management in the 21^{st} century

Biophysical site index models can provide reliable predictions of site quality based on a large array of climatic, topographic and soil biochemical variables and they help to identify which are the most significant factors that affect tree growth. However, their limitation arises from the fact that they remain statistical models. As such, they tend not to be applicable outside the collection data range, increasing the need for extensive and costly field surveys which must include the whole variability of the measured variables. Additionally, because they are statistical models their portability between species or even for the same species but in totally different site conditions, is limited. Furthermore, they are not capable of providing an understanding of why changes in one of the independent variables affects the dependent variable, as no real process (on either biochemical or physiological level) is adequately represented. Although they can be very reliable management tools, the lack of explicit process representations makes them less adaptable to changes in either soil chemistry (e.g., increases in nutritional status or soil water holding capacity) or changes in climate (e.g., increases in mean air temperature or precipitation). However, forest policies today are driven by international laws and agreements such as the Kyoto Protocol. Thus the argument would be

that relevant decisions should be based on a tool portable amongst growing conditions and species, capable of providing reliable answers, and process-based models could successfully fulfil such a role.

1.6.3 Ecological Site Classification

Demand for a site classification scheme based on ecological principles lead to the development of the Ecological Site Classification (ESC) for Great Britain (Pyatt *et al.*, 2001). ESC is a site classification system based on the assessment of soil nutrient and moisture status through relationships with ground vegetation and humus type (Wilson *et al.*, 2001, 2005). ESC is essentially a biophysical model, capable of including climatic factors such as accumulated temperature ($\mathrm{Day-Degrees} > 5^{\mathrm{o}}\mathrm{C}$), moisture deficit, windiness and continentality, together with soil characteristics such as soil texture, depth, rootiness and stoniness and with ground vegetation, to provide estimates of soil moisture regime (SMR) and soil nutrient regime (SNR). ESC provides estimates of site species suitability and woodland communities based on those soil and climatic characteristics, together with a prediction of potential tree growth. ESC has been integrated under a GIS framework (Ray, 2001), providing regional estimates of soil nutrient and moisture status as well as spatial variability of species suitability and potential yield increment.

1.6.4 Population dynamics models

Among population dynamics models (or gap models, as they are widely known), the most widely known is JABOWA (Botkin *et al.*, 1972), which has been the basis for the development of many other gap models, such as FORCAT (Waldrop *et al.*, 1986), FORDACK (Kruse and Porter, 1994), FORMIS (Shugard, 1984), FORSKA (Leemans and Prentice, 1987), GROWEST (Fitzpatrick and Nix, 1970) and PICUS (Lexer *et al.*, 2001). These models simulate the dynamics of individual trees, their recruitment, growth and mortality based on a series of either deterministic or stochastic functions. Gap models are based on individual trees forming a certain plot. Tree interactions alter

the environment within the plot up to a distance similar to the site of the gap created by the removal of trees either by thinning or by natural mortality. Their general structure includes initial values for climatic variables, initial number of trees and species composition, with a growth sub-model predicting growth of diameter and volume for each tree and a recruitment sub-model estimating the number of recruited trees. The mortality sub-model calculate the reduction in the number of trees from the population where a resource limits growth using a series of external factors (multipliers) that range from 0 to 1, as estimated within an additional resource sub-model. (Waring and Running, 2001). Outputs include species composition, size distribution and age structure. The disadvantage of such models is that growth and effects of environment are again represented through a series of empirical functions, lacking any representation of photosynthesis, respiration and carbohydrate allocation to structural tree components. Some recent models have however integrated gap models with process-based models (Zuo *et al*., 2003; Seidl *et al*., 2005) to provide predictions of species composition and age structure distribution based on the known physiological functions.

1.6.5 Process-based models

Process-based models are defined as a process in which the behaviour of a system is defined through a set of functions based on physiological and mechanistic processes occurring over time (Mäkelä, 2003). The complexity of the algorithmic representation is in most occasions very high. Process-based models simulate the production of a single tree or a stand by utilising inputs such as mean temperature, rainfall and solar radiation. They simulate process as such as photosynthesis, respiration, biomass allocation, nutrient utilisation and uptake, litterfall and root turnover based on physiological principles (McMurtrie *et al*., 1992, BIOMASS) or biochemical principles (Running and Gower, 1991, FOREST-BGC) at a very fine time scale (hours, days). The complexity of the models depends on the modelling resolution, that is the level at which it operates, e.g., leaf, tree, stand, region or globe. Models which simulate at a fine temporal scale (e.g., hour) and at a very fine resolution (e.g., leaf) have a larger parameter vector necessary for parameterisation and initialisation. To obtain a fairly

simple model with reduced generality, but with the same physiological principles, then the option is to increase the resolution and the time step. Such models can be useful as tools not only for research but for management too (Johnsen *et al*., 2001). Models differ among each other on the way the main processes are represented. For example BIOMASS (McMurtrie *et al*., 1992) and MAESTRO (Wang and Jarvis, 1990a,b) represent photosynthesis with a detailed description of canopy architecture, where 3-PG (Landsberg and Waring, 1997) assumes a one-layer canopy. Even such detailed models as BIOMASS and MAESTRO differ between them in the way photosynthesis is modelled. MAESTRO can include different canopy shapes calculated in an extremely detailed mathematical way of estimating the architecture of canopy in contrast with BIOMASS, which assumed three layer of canopy with equal shape.

Compartment process-based models (Monserud, 2003) represent ecosystem as a system of pools (else known as compartments) with the intention of predicting in-fluxes and out-fluxes from the compartments unit per time step (Parton *et al*., 1988; Running and Coughlan, 1988; Aber *et al*., 1992; McMurtrie *et al*., 1992; Landsberg and Waring, 1997, see also figure 4.1). The first process-based models such as FOREST-BGC and CENTURY appeared in 1988 (Parton *et al*., 1988; Running and Coughlan, 1988) but since then the demand for more closed forest models based on flux predictions (Landsberg *et al*., 1991) has lead to the development of many other well tested and established models, such as BIOMASS (McMurtrie *et al*., 1990), MAESTRO (Wang and Jarvis, 1990a,b), RothC (Jenkinson, 1990), GENDER (Moorhead, 1991), Edinburgh Forest Model (Thornley, 1991), PnET (Aber *et al*., 1992), G'DAY (Comins and McMurtrie, 1993), ICBM (Andrén and Kätterer, 1997), PROMOD (Battaglia and Sands, 1997), 3-PG (Landsberg and Waring, 1997), FinnFor (Kellomäki and Väisänen, 1997), Pipestem (Valentine *et al*., 1997), FullCAM (Richards, 2001), YASSO (Liski *et al*., 2005) and many others.

1.6.5.1 Overview of some existing process-based models

By reviewing the existing literature one can find a wide range of process-based models, each one with its own level of complexity, assumptions and main principles, but

somehow all representing the basic physiological functions. Here, we provide a brief overview of some of the most well known models, with the intention to demonstrate their philosophy and applications.

1.6.5.1.1 FOREST-BGC

FOREST-BGC first appeared in the literature in 1988 (Running and Coughlan, 1988), while the newer version was presented by Running and Gower (1991). Since then, it has been evaluated across several biomes and climatic conditions, with changes leading the development of the model into what is known today as BIOME-BGC. FOREST-BGC has three major pools for carbon and nitrogen for each structural tissue i.e., leaf, stem and roots, where net photosynthesis is allocated. Maintenance respiration, photosynthesis, evaporation, transpiration and water inflow and outflow are estimated on a daily basis, whereas soil carbon and nitrogen stocks, decomposition, nitrogen uptake, growth respiration, root and leaf turnover and carbon allocation are estimated on a yearly or monthly basis. The model considers leaf area index as a key structural attribute with a significant control over several processes. Carbon and nitrogen pools are dependent on organic matter decomposition rates, which in turn, depend on nitrogen concentration in the tissue and soil temperature. Nitrogen uptake is estimated by multiplying the concentration of leaf nitrogen and root nitrogen with their growth rates, respectively. The model utilises the philosophy of environmental modifiers on growth. Photosynthesis is constrained through a series of modifiers ranging from 0 to 1, such as temperature and soil water potentials to account for environmental limitations. Modifiers are estimated through well established relationships, such as Beer's law and Penman-Monteith equation.

The model with its newest form of BIOME-BGC has been applied in Austria (Pietsch *et al*., 2005) for several species including Scots pine, oak, beech and larch, in the Mediterranean region for coppice oaks (*Quercus ilex* L.) to investigate the carbon and water flow (Hoff *et al*., 2002), in southern France for investigating the effects of climate change and CO_2 increase on growth of Aleppo pine (*Pinus halepensis* P. Mill.,

Rathgeber *et al.*, 2003), in North America and more specifically in Oregon (Running, 1994), Alaska and north-west Canada (Keyser *et al.*, 2000) for the assessment of carbon balance under a climate change scenario. Other applications of the model include an investigation of climate change on forest growth in Austria (Hasenauer *et al.*, 1999) and an investigation of the effect of disturbance and climate on water and carbon budgets of evergreen forests in the U.S.A. (Thornton *et al.*, 2002). Finally the model has also been applied at a global scale (Hunt *et al.*, 1996) for assessing global patterns of net carbon exchange.

Although it represents all processes of an ecosystem, the model does not have the mathematical complexity of models such as the Edinburgh Forest Model or MAESTRO, as the application of modifiers simplifies calculations. Nevertheless it retains a high level of complexity due to a large number of parameters necessary.

1.6.5.1.2 Edinburgh Forest Model

The Edinburgh Forest Model was presented by Thornley (1991) based on a transport-resistance approach to carbohydrate partitioning. It operates at a stand level and for monoculture stands. All major processes are represented in the model, using five major organ compartments, i.e., foliage, branches, stem, coarse and fine root and mycorrhizae. It has a daily time step and it utilises inputs of daily solar radiation and daylength, daily soil and air temperature and CO_2 concentration. Each structural compartment is separated into meristem, structure, carbon substrate and nitrogen substrate, whereas death of roots and other litter provide carbon and nitrogen for the soil pools from which uptake of nitrate and ammonium occurs. A modification of the model's nitrogen cycle was later introduced by Thornley and Cannell (1992). Many applications of the model can be found in the literature, with most importantly the application in Scottish climate (Thornley and Cannell, 2000), where an investigation was conducted to determine the effects of different thinning scenarios on carbon and timber production accumulation. The scenarios included an undisturbed forest, a removal of biomass between 0.2 - 40%, the removal of 50% of the total woody biomass and a clear-felling

with replanting. Amongst their findings was that undisturbed stands had higher carbon accumulation, however moderate thinning regimes gave high timber yields and high carbon storage. The importance of continuous cover forestry was highlighted as the most significant result to achieve the best combination of high yields and high carbon storage. Another application of the model (Cannell *et al*., 1998) investigated the effect of nitrogen deposition combined with a climate scenario including an increase in CO_2 and found that the combined effect could almost double the growth of conifers in the UK.

The model is a complete mathematical representation of the carbon and nitrogen cycles, however there is a large array of initial state variables and parameters which demand a large number of data for parametererisation and validation of the model. Its accuracy and complexity in representing mechanistic processes of tree growth and soil decomposition makes it a very useful tool for research, however its application to forest management is almost prohibited.

1.6.5.1.3 MAESTRO

The model was developed by Wang and Jarvis (1990a) as a result of an effort to model canopy photosynthetic processes. MAESTRO is an array model, which simulates individual crowns of trees in a stand and the stand as a whole. It utilises a series of mathematical algorithms representing geometric properties of leaf, twigs, branches and trunk and how they affect radiation absorption, photosynthesis and transpiration. It is a crown architecture oriented model, where photosynthesis is affected by crown's shape, total leaf area, leaf spatial distribution within the crown and leaf inclination with regards to solar radiation. Although Wang and Jarvis (1990a,b) tested the model against data of photosynthetic active radiation, subsequently applications have remained limited to research. Medlyn (1998) used the model to investigate if the canopy is structured in such a way that most leaves are exposed to non-saturating quantum flux density (resulting in a linear relationship of canopy photosynthesis with photosynthetic active radiation) and if the variability of the light use efficiency is dependent on the time and spatial

scale. Despite its mathematical complexity, there has been an effort of integrating the model with a growth and yield model PTAEDA2, in an investigation of the effected environmental change on the growth and yield of lodgepole pine (Baldwin *et al*., 2001). Despite the difference in philosophy between the two, the models were integrated using the outputs of net photosynthesis gain from MAESTRO as site index from PTAEDA2, to provide the dynamic linkage. Nevertheless, the complexity of MAESTRO makes any further development of such integration difficult.

1.6.5.1.4 BIOMASS

BIOMASS (McMurtrie *et al*., 1990) is amongst the first models using quantum yield efficiency to derive gross primary production. Photosynthesis is modelled through a canopy model, where by light interception of both direct and diffuse radiation depends upon canopy architecture, using three horizontal canopy layers of equal depth with the assumption that tree crowns are all identical in shape. The photosynthetic capacity of each layer is estimated from scatter and direct radiation and then integrated to provide estimates of photosynthesis for the whole stand. The model uses daily time steps at the stand level, requiring daily weather inputs of maximum and minimum air temperature and rainfall and other characteristics such as longitude, latitude, root-zone depth and volumetric water-content. Water balance is estimated through the Penman-Monteith equation, while the effect of environment on growth comes as in FOREST-BGC through a series of environmental modifiers reducing photosynthesis.

BIOMASS, together with FOREST-BGC, are probably the most widely used process-based model applied for research. McMurtrie *et al*. (1992) used the model to explore the effects of water and nutrient availability on the growth and carbon partitioning of *Pinus radiata* D. Don., whereas Zheng *et al*. (2002) used the model to investigate the effects of climate change on the production of *Picea abies* (L.) Karst. in South-West Norway, while Bergh *et al*. (2003) expanded the same investigation for both coniferous and broadleaved species, such as beech and poplar in the Nordic region. BIOMASS has also been used for eucalypt species in south-western Australia in an investigation

of the growth patterns on ex-farmland areas (Hingston *et al*., 1998).

1.6.5.1.5 CENTURY

One of the most popular soil organic matter decomposition models was developed by Parton *et al*. (1988). CENTURY is a model originally developed for grasslands but successfully transferred in application for forests, agricultural crops and savannah. It runs at a monthly time step and utilises monthly values of maximum and minimum temperature and precipitation. It has two forms of litter, one metabolic and one structural, with three soil organic matter pools, i.e., active, slow and passive, each one with different decomposition rates. Soil texture, has also an effect on decomposition. Foliage litter is directed to the metabolic and structural litter pools together with fine root litter, which then enter the active carbon pool. Branches and other coarse woody litter are directed to the slow decomposition pool, while carbon is allocated to and from the resistant pool. Available mineral nitrogen is estimated from carbon pools through C:N ratios, from which leaching losses and mycorrhizal uptake is estimated and nitrogen inputs can be added. Mineral nitrogen is also uptake by plants for growth. The model has been used in several occasions such as the study by Moorhead (1991) for northern Chihuahuan Desert, or a boreal forest transect in central Canada (Peng *et al*., 1998) or for a synthesis study using a global dataset from Norway, Canada and the U.S.A. (Kirschbaum and Paul, 2002). However, the increased number of parameters necessary does not allow a complete integration with an equally complex tree physiological model, such as BIOMASS or FOREST-BGC, for management purposes.

1.6.5.1.6 3-PG

The model was presented by Landsberg and Waring (1997) and it can be considered a much simplified version of the BIOMASS model. 3-PG (Physiological Principles of Predicting Growth) follows the same basic principles of BIOMASS, that is, a quantum yield efficiency constrained by a series of environmental modifiers. Adoption of other

assumptions, such as the fixed ratio between gross and net primary production, removes the need for a respiration sub-model, and a canopy photosynthesis sub-model which simplifies its application. In addition, the inclusion of variables such as mean annual increment and basal area makes the model more ”forest manager” friendly. A more detailed description of the model's principles and a comprehensive literature review of its application is presented in Chapter 4 of this thesis.

1.6.5.1.7 ICBM

The Introductory Carbon Balance Model is a simplified soil organic matter decomposition model, which follows the same principles as CENTURY but with the simplifying philosophy of 3-PG. The model was introduced by Andrén and Kätterer (1997), as a simple soil carbon balance model for agricultural use. Kätterer and Andrén (1999) used ICBM to investigate the influence of management on soil carbon stocks for agricultural fields in Northern Europe. On the other hand, Andrén *et al*. (2001) used ICBM to investigate the influence of soil fauna on soil carbon balance. Finally, Kätterer and Andrén (2001) used the ICBM family in a series of experiments to evaluate their use. The first and most simple version of the model included two carbon pools as initial state variables, one ”young” for the freshly decomposed litter and one ”old” for the humified litter. It included five parameters, of which two are constant decomposition rates, a humification coefficient representing the rate of which carbon enters the old pool and a parameter for representing the external response of decomposition. For more details see Chapter 4.

1.6.6 Process-based models and forest management

Mäkelä and Vanninen (2000) supported the view that decision-making in forest management is gradually moving towards analytical approaches and that process-oriented components will gradually be used by forestry enterprises. This is well demonstrated as process-based models have been used for investigating the effects of current management techniques on carbon budget and timber production (Liski *et al*., 2001; Kar-

jalainen *et al*., 2002; Kaipainen *et al*., 2004; Blanco *et al*., 2005), the effects of climate change on timber production (Kellomäki *et al*., 1997), the effects of management on stem size distribution (Landsberg *et al*., 2005) or the effects of afforestation on soil carbon (Paul *et al*., 2003b).

The last few years have seen an extensive effort to introduce process-based models as a useful forest management tool (Landsberg and Waring, 1997; Battaglia and Sands, 1998; Johnsen *et al*., 2001; Landsberg *et al*., 2003; Landsberg, 2003b,a; Mäkelä, 2003), while Monserud (2003) supported the view that process-based models could provide the necessary tool to establish sustainability of forest production for the whole ecosystem.

Johnsen *et al*. (2001) discussed the applicability of process-based models in forest management and concluded that understanding the interactions between foliage nutrient dynamics, site fertility and soil nutrient availability is the major limitation of process-based models, but also the great challenge to modellers, as it makes very difficult the task to predict growth accurately using soil nutritional dynamics. The difficulty in modelling nutrient dynamics in the closed tree-soil system was highlighted much earlier by Landsberg *et al*. (1991). They suggested that a way of including nutrient modelling would be by modelling uptake of nitrogen as the product of the annual production of tissues by their respective nitrogen concentrations. This theory was demonstrated by Landsberg (1986). An alternative approach would be to estimate mineralisation of nitrogen in the soil and then calculate the uptake by actually removing quantities from the soil (Landsberg *et al*., 1991). One of the first attempts to include a complete organic matter decomposition sub-model within a process-based model was demonstrated by Running and Gower (1991) who utilised nitrogen concentration in leaves and roots to determine stand nitrogen demands. Apart from this effort however, there was a failure in introducing a simple soil process-based model integrated within a complete ecosystem model. Only recently, has attention turned to integrating separate and well established soil decomposition sub-models with either tree-level or stand-level physiological models (Liu *et al*., 2002; Peng *et al*., 2002; Paul *et al*., 2003a; Hirsch *et al*., 2004; Paul and Polglase, 2004). Obviously, this integration increases the complexity

of such models and makes their use for management very difficult. The solution would be a simplistic, complete ecosystem process-based model.

1.6.6.1 The simplified process based model 3-PG in a forest management context

Battaglia and Sands (1998) also supported the idea that process-based models can be useful tools for forest management, however they also discussed the issues of resolution, complexity and generality. They highlight five major and very important points that need to be considered for such models before their use, that is, (i) their spatial and temporal resolution, (ii) the number of state variables, processes and parameters in the model, (iii) the balance between *"empiricism and phenomenology in the manner in which processes are represented"*(Battaglia and Sands, 1998) (iv) the details of the inputs required for the model to run and finally (v) the nature of the outputs and how valuable they are according to their use. Most process-based models work at very fine spatial and temporal scales. MAESTRO works at the tree level with a very fine temporal resolution (hours). On the other hand, FOREST-BGC (BIOME-BGC) and BIOMASS run at the stand scale but their temporal scale is days, although the fact that FOREST-BGC runs some of its functions at a yearly time step adds a very interesting perspective. Nevertheless, it is still considered very detailed. CENTURY on the other hand has a much more coarse temporal scale (month), while the number of state variables, processes or parameters necessary is still very high. The number would be even higher if it were combined with a model such as BIOMASS. The Edinburgh Forest Model, similar to MAESTRO, represents processes in a very detailed manner. BIOMASS and FOREST-BGC on the other hand, have a more simplified phenomenology but need highly detailed inputs such as daily maximum and minimum temperature, precipitation and solar radiation. Finally, most of the well known process-based models have a large array of variables useful for carbon budgeting and for an eco-physiological understanding of forest ecosystems, but do not provide variables meaningful to forest managers. Battaglia and Sands (1998) suggested that the best process-based model should fulfil all the above aspects in the best possible way, by compromising some of its complexity in favour of generality so as to reduce the demand for parameters

and initial state variables. Additionally, an increased temporal resolution will increase the generality and the applicability of process-based models for forest management. Battaglia and Sands (1998) also supports that lumped-parameter process-based models and hybrid models (i.e., models which include process-based routines with integrated empirical relationships) could provide the way in which our understanding of physiological processes could be included in forest management.

3-PG and ICBM/2N (see Chapter 4 for general description of the two models) can fulfil all the above. Both models operate at the stand scale although larger spatial scales are possible after integration with GIS (see below). Both models operate under a relative coarse temporal scale, that is monthly (although ICBM/2N can operate with yearly time steps, see also Chapter 4), which demands less detailed meteorological inputs, i.e., monthly averages of maximum and minimum air temperature, precipitation and solar radiation. Empiricism is also included in the model, as 3-PG simulates respiratory losses through a constant ratio between gross and net primary production (Waring *et al*., 1998), while it avoids the need for a complex canopy photosynthesis sub-model by introducing maximum quantum yield efficiency to estimate solar radiation conversion into tissues. Allocation patterns are also represented through empirical allometric equations, while natural mortality is accounted through the well established self thinning law. Thus, although it still maintains the representation of processes (e.g., photosynthesis, allocation, mortality), the empirical relationships reduce the number of parameters and initial values necessary. In addition, the option of estimating stand volume, basal area and mean annual increment through empirical allometric relationships and include them as standard outputs of the model makes it applicable for forest management. In the same way ICBM/2N introduces only three soil carbon pools capable. It estimate decomposition decomposition rates modulated by environmental factors, while nutritional effects (mainly nitrogen) are estimated through simple C:N ratios. The combination of those two models produce a relative simple ecosystem model capable to fulfil any current management objective (although ICBM/2N can operate with yearly time steps, see also Chapter 4), which demands less detailed meteorological inputs, i.e. monthly averages of maximum and minimum air temperature, precipitation and solar radiation. Empiricism is also included in the model, as 3-PG simulates

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Moreover, according to Robinson and Monserud (2003), forest growth models should follow certain criteria in order to assess their adaptability and applicability across the world forests. More analytically, criteria for adaptability of models should include: 1) Portability, 2) Site-specific adjustments, 3) Extendibility, 4) Source code availability, 5) Cost, 6) Documented fit, 7) Interface, 8) Variety of sample designs, 9) Submodels and 10) Outputs.

First, portability indicates how easy it is for a model to adapt into new management situations, different geographic areas or different species. This is straightforward with 3-PG, as it includes many site-specific parameter such as latitude, weather data and soil texture, whereas the species-specific parameters such as allometric coefficients and maximum yield quantum efficiency make it applicable for several species. In this way, any site specific adjustments are introduced in the parameter set. Additionally, a local calibration set will adjust any theoretical physiological, species-specific parameters which will include any site effects. Of course, the question arise of how site-specific adjustments can be introduced in the context of a high spatial resolution study. An an-

swer to this could be application of an intra-site parameter set, capable of representing adequately all parameter variability across site conditions (see also Chapter 4 and 6). Development of such parameters sets could be developed with the use of modern computational techniques, such as Markov Chain Monte Carlo simulations and Bayesian calibration (Van Oijen *et al*., 2005, see also Chapter 4). Extendibility on the other hand is explained as the ability of the model to include new modules and new routines. With 3-PG, this can be done as modules can be added or removed according to the specific projects objectives (see also Chapter 4), as the source code is freely available over the internet. This makes the model adaptable to any new developments, whereas new knowledge could easily be incorporated into existing model routines. Since 3-PG's source code is freely available, this is no extra cost required into developing applications fulfilling specific management or research needs. Additionally, the current built-in interface within a spreadsheet makes it user and more specifically "forest manager" friendly, while the extensive testing of the model (see Chapter 4) provides a well documented fitting procedure and exploration of models internal feedbacks. Moreover, current documentation makes its use easy and understandable. 3-PG also includes a series of sub-models for management treatments such as thinning, fertilisation and irrigation. Although the model lacks soil processes, an integration with ICBM/2N could fill the gap, so as to include any possible soil treatment effects on productions. The absence of a silvicultural sub-model within 3-PG makes it less applicable and adaptable to any non monoculture, even-age plantations. Recent developments however, have integrated 3-PG with well established gap models, such as PICUS (Seidl *et al*., 2005) and GROWEST (Zuo *et al*., 2003), to complete its adaptability over a more natural forest environments. Finally, very important is 3-PG's capability of producing outputs of standing volume and mean annual increment, which extend its adaptability from a clear research to a forest management tool (Almeida *et al*., 2004).

1.7 Spatial models for forest management and research

Natural resources are geographically distributed. That makes natural resource management and especially forest management, a geographic problem. In order to secure

sustainable use of the forests, managers need to know what is growing where, how much, what are the needs, what are the conflicts between the demands, etc. Before the construction of a forest road, information such as what are the tree and flora species in the forest, where and what will be the impacts of the road to the forest, are crucial. To secure annual yield of timber from the forest, managers need to know how much timber is in each stand, how far one has to go to get it and how expensive will be the extraction. Finally the recreation demands need to be satisfied, without having all the negative impacts of timber extraction. Those are some examples of problems that a forest manager faces and whose solutions are geographic.

Until the last few decades, the only available tools for solving geographic problems were paper maps. They were very useful, and they still are one of the most important parts of a management plan. But certain things make them difficult to use. According to Burrough and McDonell (1998), these include:

- The original data are reduced in volume or classified in order to make the maps more understandable and representable, thereby loosing many local details.
- The drawing must be precise and accurate particularly for complex themes, which increase the possibility of errors.
- For the representation of a large volume of information for an area, a number of map sheets is required. When the area of interest is near the junction of maps this makes it more difficult to read.
- Once the data are in the map, it is very difficult and costly to retrieve information and combine them with other spatial data.
- The paper maps are qualitative static documents, which makes it difficult to implement any quantitative spatial analysis.

On the other hand, making any type of decisions about the forest requires a large amount of information including mean height, stand diameter, stand age, site index, standing volume, soils and rock layer, vegetation type, canopy closure, paths and roads

etc. Storing and maintaining however, all the information to on a paper database and been presented into maps, was an expensive and time consuming process. Finally, querying and manipulating data on such databases and linking information on maps was also very difficult.

Today, new technology and especially computer science, offers a solution to all the difficulties that paper maps and paper databases present. That is the Geographic Information System (GIS). Since the mid 1960s, when the first GIS was created by the Canadian Geographic Information System, there has been a huge improvement in map construction techniques, database manipulation and spatial analysis. GIS offers the opportunity of data linkage with digital maps and spatial analysis, like buffering, measurements, slope and aspect maps, contouring. Also offers data manipulation (table and map algebra), geostatistics and the opportunity of modelling and visualisation of the past, present and future status of the resource. Modelling is one of the most important uses of GIS, because it provides the manager with the ability to have a visual version of the current, past or future situation of an area. Finally, digital databases make queries and data manipulation easier and cheaper, as well as maintaining and updating them easy, fast and accurate. Significant was also the contribution of the development of new ways of data collection from the field or from other sources, such as:

- Global Positioning Systems (GPS)
- Field surveys with hand GIS
- Scanning of maps and photographs for digitising and rasterisation
- Remote sensing (orthophotographs, aerial photographs, satellite images)
- On screen digitising
- Photogrammetry
- The World Wide Web (webGIS)

1.7.1 Definition of Geographic Information Systems

Several definitions can be found in the literature about Geographic Information System. There are: toolbox - based definitions, database-based definitions, or organisation-based definitions (Burrough and McDonell, 1998). A toolbox - based definition states that GIS are *"a powerful set of tools for collection, storing, retrieving at will, transforming and displaying spatial data from the real world"* (Burrough 1986, cited by Burrough and McDonell, 1998).

Another definition by Parker (1988) (cited by Burrough and McDonell, 1998) tells us that GIS are *"an information technology, which stores, analyses and displays both spatial and non-spatial data"*.This definition can perfectly explain the use of GIS in forestry. Experience however, tells that not many countries or forestry agencies have fully understood the analysis capabilities of a GIS. A database-based definition says that a GIS is

> *"A database system in which most of the data is spatially indexed, and upon which a set of procedures operate, in order to answer queries about spatial entities in the database"*

(Smith *et al*. 1987, according to Burrough and McDonell, 1998). Finally, an organisation - based definition is thatGIS is *"a decision support system, involving the integration of spatially referenced data in a problem solving environment"* (Cowen (1988), according to Burrough and McDonell, 1998).

But despite all the above mentioned definitions, GIS remain a very useful decision support tool and a great help to everyone, from big companies and scientists to individual citizens, facing problems that include spatial and non - spatial data, by analysing them in such a way that can support any future decision. A dangerous trap, in which the GIS user must not fall, is that GIS does not solve the problem, but merely provides one of the possible solutions, according to the data the users gave for analysis.

1.7.2 Environmental modelling

GIS, besides the advanced capabilities of spatial analysis that they offer, give the natural resource managers and scientists the opportunity to model the resources in a virtual two or three-dimensional world, in order to better visualise environmental or management problems and reach the best solution. According to Burrough and McDonell (1998) a model is *" a representation of attributes of features of the earth's surface in a digital database"* or *"a set of algorithms written in a computer code that describe a given physical process or natural phenomenon of the earth's surface"*.

So a model is a tool to offer *"representation to help us assemble far more knowledge about earth than is possible on our own"* (Longley *et al*., 2001). According to others

> *"a model is a tool used by scientists and decision makers to abstract from reality those components that are most germane to their problem domain ...the process of abstraction is to reduce the complexity of the real world to a manageable level"*

(Bennet *et al*. 1996, cited by Burrough and McDonell, 1998)

In forestry more specifically, Feng and Chen (1996) suggest that

> *" GIS-based spatial analysis of forest stand structure and volume estimation data are analysed to be a rich, accurate and efficient information, which information can be used for explaining, estimating and predicting"*.

Surely, environmental modelling offers the desirable option of the visual representation of the environment and resources, but more importantly it offer simpler and more manageable information on what are the resources, what is the spatial relation between them and further more, a classification by attributes that describe them (stand volume, height, diameter, net primary production, net ecosystem production). Environmental models can also represent the present or even the past condition of the resources (conceptual models).

1.7.2.1 Environmental modelling for forest management

It is obvious that, because of the spatial distribution of the resources on the earth's surface, natural resources management is, in final analysis, a geographical problem. Forests may stretch to thousands of hectares while rivers and lakes may extend to thousands of meters. GIS find many applications to a number of sectors of natural resource management, either as a simple mapping tool or as an advanced spatial analysis tool. Some of the sectors of natural resource management that GIS software and applications find use are:

- Agriculture
- Forestry
- Oil industry
- Conservation
- Wildlife management
- Water management

GIS can be used in forest management, among others, for:

- Fire management and control
- Strategic planning
- Road planning and forest access
- Silvicultural activities

Although it is not possible here to provide a thorough examination of the applicability of GIS in forest management, same examples are provided.

1.7.2.1.1 Fire management and control

GIS can be used for understanding the direction, speed, intensity, fuel loads and tracking of burned areas and equipment. It can also be used to map where the highly danger areas are according to certain set of rules and criteria. The whole fire extinguishing operation can be coordinated by the use of GIS, by knowing where the fire is, where the closest fire faucet are, so that firemen and vehicles can be placed. Finally, it can help to understand how to prevent the starting of fires so that next season planning can take place.

1.7.2.1.2 Strategic planning

GIS can help in the strategic planning for forest resources. It can store large amounts of information (spatial and non-spatial), create topographic, hydrographic and vegetation maps. Several spatial analyses can help the forecasting and planning activities, like creating erosion maps, in order to identify possible degradation areas and prioritise the planting.

1.7.2.1.3 Road planning and forest access

With a GIS, is possible an easy visualisation of the impacts of road construction on the forest environment is possible. With a network analysis, decisions can be made of where to place the roads, so that they will be useful, cheap, with less environmental impact, close to timber extraction and recreation areas, and away from high sensitivity, conservation areas.

1.7.2.1.4 Silvicultural activities

With a GIS, the manager can keep track of all silvicultural treatments operated in the forest and co-ordinate them in such a way that they will not come into conflict with

recreation areas and activities.

1.7.2.2 Environmental modelling for scientific research

Environmental modelling can also be used for scientific purposes. Exploration of climate change impacts on photosynthetic productivity and net ecosystem productivity (Ehman *et al*., 2002; Berthelot *et al*., 2002), modelling of P_G (Williams *et al*., 2001) and P_N (Jiang *et al*., 1999; Mickler *et al*., 2002a,b), forest biomass (Brown *et al*., 1999), site index (Bateman and Lovett, 1998; Mitsuda *et al*., 2001; Swenson *et al*., 2005) or generally growth and yield (Ditzer *et al*., 2000; Tickle *et al*., 2001a,b) are some of the examples. GIS can provide the necessary spatial modelling to explore topographic and geographic factors affecting physiological processes.

Bateman and Lovett (1998) developed yield class models from field data using principal component regression analysis and extrapolated the results utilising spatially interpolated data of elevation within a GIS framework, producing in such a way maps of potential yield class for Sitka Spruce. In a similar way, Mitsuda *et al*. (2001) developed a multiple linear site index model from a set of ground data, with elevation as one of the independent variables and later producing spatial surfaces of site index using a Digital Elevation Model. On the other hand, Ditzer *et al*. (2000) used GIS to analyse field data for the investigation of growth of a tropical rain forest using the process-based model Formix 3-Q. Analyses included the construction of a classification scheme for site quality, slope and forest structure, which later were incorporated with field measurements of stand biomass to provide the bases for simulations in an investigation of thinning regimes and current harvesting scenarios on sustainable forest management and undisturbed regeneration of the logged-over forest areas.

1.7.2.3 Methods of spatial environmental modelling

1.7.2.3.1 Vector based modelling

Vector data models ”represent space as a series of discrete entities - defined point line of polygon units, which are geographically referenced by Cartesian co-ordinates” (Burrough and McDonell, 1998). In other words, there are simple points with (x, y) co-ordinates, connected with lines, creating discrete objects like polygons. Vector data can be used in environmental modelling with vector algebra, that is, using mathematical models for each point, creating a new database. Vector algebra implements basic statistical and mathematical operations.

1.7.2.3.2 Raster based modelling

Raster data models are representations in a cell-based form. ”All geographic variations is expressed by assigning properties or attributes to these cells” (Longley *et al.*, 2001), i.e., certain geographic entities (e.g., forest stands) are expressed by a number of equal size cells, where each cell has a value (altitude of the stand, slope, volume, height, diameter, etc.). Raster data are used in environmental modelling with map algebra. Raster data can come from vector data, by giving a cell the value of one of the vector information following the X and Y’s (interpolation) or by remote sensing techniques, which make them more accurate (satellite images, aerial photographs).

1.7.2.3.2.1 Map algebra

One of the most basic spatial analysis of raster data is map algebra. Because of the cell-based form of raster maps, it gives the GIS users the ability of applying simple or complex mathematical or statistical operations on a cell base. In other words, the value of one cell can be entered in an algorithm or even to be added in an algorithm with the values or other cells from the same of other map layers and produce a new map with

cell values. The value of the new cell is the result of the algorithm For instance:

$$NewMap = \left[\frac{Map\,1 + Map\,2}{Map\,3}\right] \times Map\,4$$

Algorithms can include all mathematical and Boolean operations. Functions in map algebra can be:

- Local, when the value of a cell in a map is a function of the value of the same cell of Map 2.
- Focal, when the value of a cell in a map is a function of the value of other cells of the same map.
- Zonal, when the value of a cell in a map is a function of the values of a zone of cells of the same map.
- Global, when the value of a cell in a map is a function of the values of the all the cells of the same map.

The result of map calculation is a new overlaid map, with the calculated values. Map algebra can be implemented also with a cell value and a constant. In that case, the GIS takes the constant as a grid layer, where each cell had the constant as a value and it puts it into the function. Map algebra can take place either by existing software of by computer programming based on object-oriented language (e.g., Avenue). Finally, map algebra is a very useful tool for natural resource managers, using environmental modelling for decision-making, as it allows to enter complex environmental algorithms (e.g., growth models, fire models) not included in the basic GIS software, for mapping according to their needs (e.g., the fire intensity at a certain time by giving a prevalent wind grid map).

1.7.2.4 Advantages and disadvantages of vector and raster based modelling

In these two methods of modelling, there are some technical considerations related to data structure that create advantages and disadvantages in their use. These advantages and disadvantages are important in the process of modelling, affecting the easiness of handling of the data (resolution, physical size of data), and the accuracy of the representation.

According to Burrough and McDonell (1998), the advantages of vector data are as follows:

- They give a good representation of geographic entities.
- They have a compact data structure.
- They give accurate representation at all scales.
- The retrieval, generalisation and updating of the graphics are possible.
- Topology can be described explicitly.

On the other hand the disadvantages, according to the same source, include:

- They have a complex data structure.
- Overlaying several polygons requires large computer power.
- The display and plotting might be difficult and time-consuming as well as expensive.
- Spatial analysis with objects such as polygons is impossible when extra information is not included.
- Simulation modelling of processes is more difficult because each spatial entity has it own shape and form.

The advantages of raster data, always from the same source, are defined as follows:

- They are simply structured.
- Location-specific manipulation of attributes is easy.
- Many spatial analyses and filtering can be used (e.g., cell statistics).
- Mathematical modelling is very easy because of the regular shape (cell-based, e.g., map algebra).
- They are cheap in comparison to vector data because of the several ways they can be extracted (e.g., remote sensing).
- Many forms of data are available and a lot of sources provide these forms of data.

On the other hand:

- They are usually large volume data.
- Reducing resolution (cell size) reduce the accuracy of the analysis and cause loss of information.
- Transformation and calculation are time consuming and the results can produce loss of information.

By examining the advantages and disadvantages of both data forms, it is not difficult to realise that raster based modelling is far better for many technical and economic reasons leading environmental modelling applications development based entirely on raster format. As valuable as vector data can be for geographic, two-dimensional representations, the adaptability of raster data for mathematical modelling provide models of the past, present or future for better decision-making. Especially in forestry, where mathematical models are an integral part of the management (e.g., timber production), the advantages of raster data make imperative their use for forest application simulating the future and modelling different scenarios, to base present decisions for the benefit of the future.

CHAPTER 2

Bringing closer process-based and spatial modelling

2.1 A framework for model integration with GIS

The newest development of environmental modelling includes the integration of process-based models within a GIS framework. Such an integration step most often demands a high level of programming skills with either a high-level or object-oriented programming language. Nevertheless, the advantages of such integration are that spatially extended data can be utilised by the model algorithms, producing equally spatially extended outputs of ecosystem production (Coops and Waring, 2001; Tickle *et al.*, 2001a,b). The necessity for such integration arises from the fact that management has a geographical nature, although until recently only empirical models have been used, thereby losing all of the advantages of the process-based models. Additionally, the development of remote sensing has brought a wide range of accurate data (e.g., leaf area index estimation from NDVI data) for initialising, parameterising and validating models (Hunt *et al.*, 1996; Liu *et al.*, 1997; Coops *et al.*, 1998; Running *et al.*, 1999; Coops *et al.*, 2001a,b; Coops and Waring, 2001; Williams *et al.*, 2001; Chiesi *et al.*, 2002; Coops *et al.*, 2004; Swenson *et al.*, 2005; Hall *et al.*, 2006; Waring *et al.*, 2006). Furthermore, advanced spatial analysis techniques (Payn *et al.*, 1999) (e.g., geostatistical interpolation, map algebra, cluster analysis, network analysis) offered by a GIS system can be very useful tools to increase our understanding of the natural processes of ecosystem carbon accumulation and to improve management purposes.

However, any spatial implementation of process-based models or of any other forestry

or environmental model within GIS requires by a number of necessary steps as it was discussed by Fournier *et al*. (2000). Those steps include: 1) Context definition, 2) Model selection, 3) Collation of input and validation data, 4) Model-to-GIS linkage, 5) Choice of an evaluation strategy, 6) Iterative model development, 7) Application of the forecasting model. The successful spatial implementation of a process-based model with GIS depends on the successful completion of those steps.

2.1.1 Context definition

The first step includes the context definition, that is, defining the purpose of the project, objectives and milestones, sources and limitations, and finally potential users. Fournier *et al*. (2000) also argues that in this stage of the process it is necessary to define the criteria for completion of the project, the temporal and spatial scale on which the integration will work and finally define the technology and approaches adopted for the completion.

Most often criteria for completion include the successful prediction of current and future patterns. Validation of model outputs with real data is essential. For this thesis the criterion for completion was the comparison with field measurements not only during the validation procedure but also with regard to the underlining growth relationships investigated by multiple regression. Although the development of such empirical models could not provide any deeper understanding of the eco-physiological processes for the study species, they can provide a first indication of the environmental factors affecting growth. Similarities in growth patterns between environmental modelling and multiple regression approach can be interpreted as a successful completion of the integration.

Temporal and spatial resolution on the other hand, are always important consideration. The need for a thorough investigation of the spatial resolution was demonstrated by Turner *et al*. (1996). Several eco-physiological variables such as evapotranspiration and mean annual net primary production were compared with a process-based model utilising spatially interpolated climatic inputs, such as daily air temperature, precipitation, humidity, solar radiation and also inputs of leaf area index, water holding capacity

and vegetation types. The outputs were produced on a 1km and on a 50km spatial resolution and were compared with real measurements. Such an analysis demonstrated that although evapotranspiration was not affected by differences in spatial resolution, carbon fluxes were significantly different. Turner *et al*. (1996) concluded that high spatial resolution in the representation of biogeochemical processes is desirable for studies of climate change.

In practise, deciding on the temporal and spatial resolution most of the time depends not only on the accuracy of the produced outputs but also on the availability of the data inputs and calibration data, the computational capabilities and the time available (which itself is a result of the complexity of the model combined with the programming skills and language used for the integration). High-level programming languages, such as C++, need excellent programming skills, however they provide a very fast computation capacity. On the other hand, object-oriented programming under a GIS environment could be fast but also very difficult to implement. Low level programming, such as Visual Basic, R or ArcInfo AML, can provide an easier programming framework but they also significantly slow down computational time. Finally integration using ecological modelling software such as Simile (Simulistics Ltd.) and Stella (ISEE systems) limits significantly fast computational times when a fine spatial resolution is chosen.

Having made these considerations and combined with the choice of the models' time step, a spatial resolution of 1km was chosen. Model integration was completed with a high-level programming language (C++) and so computation time was significantly reduced, permitting such a high resolution. The temporal scale was set to 100 years using a monthly time step.

2.1.2 Model selection

The second step involves the identification of the model matching the project's objectives. The model must be capable to provide process-based estimation of the necessary outputs with a complexity that will not compromise computation time (see Section 1.6.6.1). Moreover the model should fulfil certain criteria, which include the adapt-

ability and portability between species and site conditions, availability of source code and easy module alteration.

For the project's objectives (see Section 1.2) the process-based models 3-PG and ICBM were used (see also Chapter 4). The two models fulfil all the necessary criteria (see Section 1.6.6.1), reduced level of complexity and temporal scale for a successful GIS integration. Additionally, the already existing integration of the model with ESRI's GIS software was considered to be a considerable advantage (ArcMap and ArcInfo) in developing a full ecosystem spatial model to be used as a tool for spatial estimates of current and future forest production.

2.1.3 Collection of input and validation data

The third step includes the establishment of test sites, data collection and model calibration. A calibration procedure demands a well established network of sampling plots, providing a series of variables as data for calibration and validation. The calibration procedure requires either the manual or automated adjustments of model's parameters, so that the model outputs match the field measurements. Climatic and topographic data are also necessary and within a spatial framework, spatial interpolation most of the times is necessary. Such interpolation can be provided for data from meteorological stations using either geostatistical interpolation techniques or empirical relationships of such climatic variables with topographic variables, such as elevation and their extrapolation is then based on those relationships using easily accessible topographic data (e.g., a Digital Elevation Model). Moreover, data inputs such as leaf area index today can be derived through remotely sensed values of NDVI. Furthermore digitised soil texture, soil type and water holding capacity maps can also provide the necessary spatial inputs.

Calibration on the other hand is one of the major components of a process-based model application. As highlighted by Janssen *et al.* (1995), calibration procedures can be limited by the nature, the amount and the quality of the available data, while the complexity of the model can also create a problematic calibration procedures. Complex

models requiring large number of parameters and inputs demand a more automated calibration as any efforts of manual calibration could be cumbersome. Janssen *et al.* (1995) also highlighted the fact that computer power, time and man-power can also be significant into introducing a high uncertainty into the calibration procedure, as they demand adequate expertise and financial resources. Such difficulties introduce an extra uncertainty into the parameters and inputs of a process-based model. Modern computation techniques, such as Bayesian calibration and Markov Chain Monte Carlo techniques (MCMC, see Chapter 4 for more details), can provide the tool to explore the uncertainty of parameters (whenever parameters values can not to be explored directly through field data) and outputs. For this project we introduced such a technique for our process-based model, as field data were frequently inadequate for calibration, validation and parameter and input estimation.

2.1.4 Model-to-GIS linkage

The fourth step includes the linkage of the model with the GIS software. There are two most common ways of coupling. The loose and the tight coupling technique. Figure 2.1 illustrates the loose coupling between GIS and the model. The two systems share databases and files either by dynamic link library files, text files or float number files. Users interact with GIS and the model with separate interfaces. Such integration methods avoid the necessity for programming skills, however they can be cumbersome when multiple files are used.

On the other hand, Figure 2.2 shows the tight coupling between GIS and model which many users have been asking for in the last few years. This method offers a common interface between GIS and model. However, such integration demands a knowledge of either a high-level programming language (e.g., C++) or an object-oriented programming language, a macro-computers language like Avenue (ArcView programming language) or Visual Basic (compatible with ArcGIS).

The question arising however, is which form of integration suits for management purposes and which for research. Experience tells us that tight coupling is the only appro-

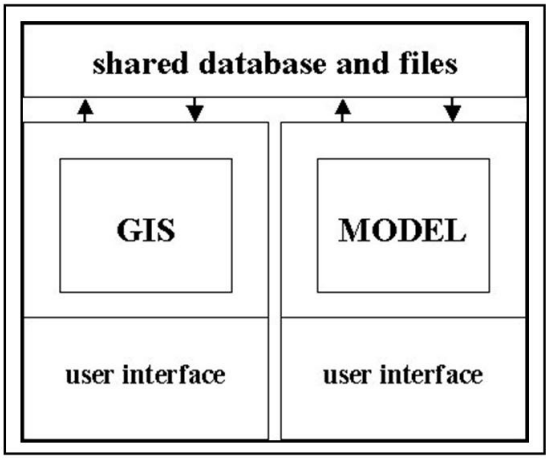

Figure 2.1: Loose and tight coupling between GIS and a model.

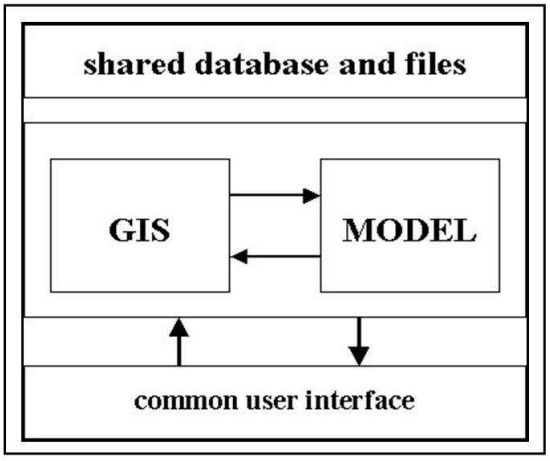

Figure 2.2: Tight coupling between GIS and a model.

priate form of integration of environmental models for management. Managers should be able to perform simple actions with the software and retrieve the output results. However in research tight coupling does not always provide the best solution. When a model is tightly coupled, it is more difficult for the user to change any of the routine of the spatial modelling procedure or the model structure itself, unless available resources and knowledge are present. In addition, when new models are about to be integrated into a GIS for research purposes then again time, resources and knowledge of object -

oriented programming are required for such integration.

An example of an environmental model fully integrated with GIS is 3-PG SPATIAL 3̀-PG SPATIALis fully coupled within ArcInfo workstation and has been used in the past for research purposes (Tickle *et al*., 2001a,b). However, it is not possible to make any changes to the existing integrated version of the model and at the same time maintain the current integration. On the other hand, loose coupling has the advantage that the user can change the functions of the model and the level of integration itself at any time, however technical problems are more likely due to software incompatibility. Thus, although tight coupling is always preferable due to less technical malfunction comparing to a loose coupling, this solution is not always the best for research purposes. Here, we integrated the models with GIS using the existing loose-coupling application of 3-PG SPATIAL (see Chapter 5).

2.1.5 Choice of an evaluation strategy

The fifth stage of the framework includes the development of an evaluation strategy for the integration. Validation is the next important step in a model application after calibration. Validation most commonly includes an independent data set with major outputs of the model and a direct comparison between observations and predictions. When incorporated in a spatial framework, such data need to be georeferenced, as spatial variation should also be included during the validation problem. Map-to-map comparison can be the answer as spatial analysis provides ways for doing so, however map errors coming from differences in the methodologies of spatial extrapolation used may lead to false conclusions. Common practise is the use of ground control points, where a network of field sampling sites across the geographical region of investigation provides georeferenced data for validation of maps.

Additionally, Medlyn *et al*. (2005) brings to the attention other problems of the validation process, such as the questions of equifinality, insensitivity and uncertainty during the validation process. Equifinality is the effect where by different model parameterisations can produce similar output results. During the validation process equifinality

could be undetectable and could lead into false conclusions. Insensitivity occurs when a model cannot capture the source of variance when compared with data obtained at different temporal or spatial scales. Finally, uncertainty arises from parameters, model structure and data structure.

In our project, validation was conducted following the ”traditional” route i.e., comparing model outputs with data from several field plots across the study region (see Chapter 4, 5 and 6) so as to include any spatial variability into the resulting parameters' vector. Furthermore, the calibration procedure based on Bayesian statistics (see Chapter 4) was conducted in such a way that spatial variation of the parameters is included in the final parameter set, while uncertainty was investigated between and within Scots pine sites across Scotland.

2.1.6 Iterative model development

The sixth step includes a continuing development and testing of the model. Although such process was not in the initial intentions of the project, continuing evaluation of both point-mode and spatial model for other species and climatic conditions may provide a further development of the model by identifying the limiting factors and prioritise development by altering or removing existing modules or adding new ones. 3-PG's iterative development is reviewed in Chapter 4 while further developments are highlighted in Chapter 7.

2.1.7 Application of the forecasting model

The final step of the spatial framework includes the application of the forecasting model. The thesis objectives are the demonstration of the integration of process-based models with GIS for forest management, providing a better understanding of the variability of Scots pine growth across Scotland and the testing of methodologies, which have the potential for the development of a classification scheme based on model's outputs. Future applications are included in Chapter 7.

2.2 Structure of the thesis

The thesis consists of four major research articles according to the aims of the project (page 2). Chapter 1 (page 1) provides an introduction into the objectives of the study, contains a thorough review of the current research of the environmental effects on forest ecosystem carbon production and timber yield and a review into the current state of process-based modelling and GIS for forest research and management. Chapter 2 (page 48) provides a discussion on the strategy arising from the aim of the thesis and on which the development of each chapter's methodology was based. Chapter 3 (page 61) presents a statistical investigation into the environmental factors affecting carbon sequestration and timber yield of Scots pine in Scotland. Chapter 4 (page 92) introduces the process-based model 3-PGN and its calibration and validation procedures, presents an investigation of the uncertainty from the estimation of the parameters and a sensitivity analysis for the exploration of the internal feedbacks between the two models. Chapter 5 (page 146) introduces the spatial version of the process-based model 3-PGN SPATIAL and its application for Scotland for an investigation of the environmental effects on the spatial variability of carbon and timber production. The chapter also proposes a new site classification scheme based on model outputs, and it provides a thorough eco-physiological investigation of the spatial variation of productivity and of its main topographic and climatic interactions. Chapter 6 (page 189) presents the application of the process-based model 3-PGN to investigate the effect of current normal management on carbon sequestration and timber production, while it provides an answer into which management option, carbon sequestration or timber, is suitable for which productivity class. Finally, Chapter 7 (page 226) provides a general discussion and final conclusions, by summarizing some of the major outcomes of the four research articles, while discussing future developments into process-based modelling for forest management.

Abstracts for the four main research articles are also presented.

Chapter 2

Scots pine is a native species widely used in commercial monoculture plantations in Great Britain. Understanding the effect of site factors on growth is vital for a successful forest management strategy. Additionally, newly developed ecosystem models such as 3-PGN demand a knowledge-base which will provide the platform for comparing model outputs with current knowledge of Scots pine growth. The study demonstrates the use of the Ecological Site Classification as a tool to classify and predict potential site productivity and presents the results of an empirical investigation into the effects of site factors on Scots pine growth based on a field survey across Scotland. Results showed a limitation of late spring - early summer drought on biomass and volume growth of eastern stands leading to a clear difference between east and west. Our data also suggest that photosynthesis occurs during winter whenever appropriate conditions are found. Winter temperatures, elevation, wind regime and soil types were also found to have a significant effect on growth. The preference of Scots pine for ammonium as the mineral form of nitrogen for growth was also highlighted.

Chapter 3

The 3-PG model (Landsberg and Waring, 1997) is a process-based model using simplified physiological concepts such as light use efficiency and a constant ratio between net and gross primary production. Also nutritional status is very much simplified with the use of a single parameter. Moreover, it is common practice of this parameter to be manually adjusted so as to fit observations. Several studies have suggested that the estimation of this parameter should come from extensive field surveys where as others demonstrated that the weakness of the model to successfully predict nutritional status has an effect on estimated gross and net productivity and that the introduction of a soil-sub model could overcome such problems. In this paper we followed the above suggestion and we introduced a soil organic matter decomposition model into the routines of 3-PG. ICBM/2N (Introductory Carbon Balance Model) was introduced by Andrén and Kätterer (1997) and followed the principal philosophy of 3-PG, which is

simplicity in representing the principal concepts of soil organic matter decomposition. The new model 3-PGN (3-PG Nitrogen) included three soil carbon and three soil nitrogen pools with eleven additional parameters. This provided a new way to account for nutritional status within 3-PG. We present both models and describe the basic concepts behind the integration. We calibrated and tested the model for commercial monocultures of Scots pine (*Pinus sylvestris* L.) in Scotland. We performed an uncertainty analysis based on Bayesian framework for ecological models and a sensitivity analysis to understand the model's feedbacks and interactions between parameters and outputs. Our results showed that the least uncertain parameters are those with a greater effect on many of 3-PGN's outputs, including quantum yield efficiency, specific leaf area and foliage:stem partitioning ratio. Although we did not find any direct effect of the soil sub-model on productivity, we found strong non-linear relationships between many of the soil parameters and 3-PGN. Root turnover rate was found to be the most uncertain parameter, whereas the ratio of net and gross primary production the least. Finally, through our validation procedure we showed that 3-PG's self-thinning routine may cause problems when predicting the number of stems in stands with low initial planting densities.

Chapter 4

Exploring current and future spatial patterns of forest production is a key aspect of the for decision making. The new role given to forests as a result of the Kyoto protocol include also carbon sequestration for climate change mitigation. Thus, knowing the temporal and spatial potentials for carbon accumulation and timber production by forests is vital. In this study we demonstrate the application of the process-based spatial model 3-PGN SPATIAL utilising spatially interpolated climatic and soil inputs to explore the temporal and spatial changes in potential timber and carbon sequestration in Scotland. Taking advantage of spatial analysis techniques, such as spatial principal component analysis and correlation analysis, we identified the effects of climatic and topographic variables on the production of Scots pine (*Pinus sylvestris* L.). Moreover, spatial regression and autocorrelation analyses were performed to identify whether the

predicted spatial outputs showed regionalised patterns and which of the climatic or topographic variables were responsible for the observed patterns. The highly regionalised spatial patterns clearly showed a difference in productivity between east and west of Scotland. Winter maximum temperature and elevation were found to be the most significant variables for ecosystem carbon accumulation, while minimum winter temperature and number of frost days were the most significant for timber production. Also a discussion is presented for the potential of utilising outputs of 3-PGN SPATIAL to develop a site classification scheme based on potential timber increment and ecosystem carbon accumulation.

Chapter 5

Under the new international laws and agreements which have come into play with the adoption of the Kyoto Protocol, forest ecosystems are now asigned with a new role, that of carbon sequestration. However, current management techniques of forest plantations (especially in Great Britain) are based on their financial viability, which focuses on maximizing timber yield and providing a stable supply. The impacts of current management techniques on carbon sequestration are not well known. In this chapter, the process-based simplified physiological model 3-PGN is introduced to provide answers to questions such as how much carbon is sequestered under the ideal scenario of normal yield and what is the effect of site conditions on growth and carbon storage of Scots pine *Pinus sylvestris* L. in Scotland. Model results showed that mean gross primary production averaged across a 100 year long rotation, ranged between 6.3 and 8.8 $\mathrm{tC\,ha^{-1}\,yr^{-1}}$, while mean net primary production averaged across the rotation ranged between 3 and 4.3 $\mathrm{tC\,ha^{-1}\,yr^{-1}}$ for yield classes between 4 and 14. Mean net ecosystem production ranged between 0.9 and 1.6 $\mathrm{tC\,ha^{-1}\,yr^{-1}}$, while maximum accumulation of carbon by the ecosystem ranged between 95.7 and 162.1 $\mathrm{tC\,ha^{-1}}$ with the maximum achieved approximately 93 years after stand establishment. The study also demonstrated a novel strategy for the construction of yield tables, based on the outputs of 3-PGN using stand volume prediction of 45 sites across Scotland and compared output results with current normal volume curves. Current yield tables are pessimistic in

their predictions of growth during several years since planting, while they tend to overestimate growth during the latest stages of a stand life. Finally, this approach allowed to provide an informed answer to the question of what is the optimal rotation length for either timber yield or carbon sequestration.

CHAPTER 3

An investigation into the variability in the growth of Scots pine across Scotland

3.1 Introduction

Great Britain's forest economy is mainly supported by a majority of commercial plantations composed of conifer species. Millions of hectares of land are planted with species such as Scots pine (*Pinus sylvestris* L.) or Sitka spruce (*Picea sitchensis* (Bong) Carr). Fast returns from relatively short rotation lengths are the main characteristics of those plantations. Scots pine is native to Scotland and it covers an area of 219,438 hectares of pure monoculture stands (Forestry Commission, National Inventory of Wooldlands and Trees, 2003), half of which is made up of native woodlands (approximately 135,313 ha, Mason *et al*., 2004). Thus, understanding the main factors affecting its growth and productivity is crucial for a successful forest management strategy.

Many studies in Great Britain (White, 1982a,b) and in Scotland (Cook *et al*., 1977; Tyler *et al*., 1996) have previously investigated the effect of a wide range of site, topographic, geological, vegetation, climatic, soil or genetic factors on timber yield utilising the statistical tool of multiple linear regression models (Cook *et al*., 1977; White, 1982a,b; Holmgren, 1994; Tyler *et al*., 1996; Fries *et al*., 1998; Fontes *et al*., 2003; Romanya and Vallejo, 2004). Other approaches employed to identify the effects of site conditions on productivity included the construction of site index curves, with either the classical relationship with stand age or including soil attributes (Elfving and

Kiviste, 1997; Palahi *et al*., 2004), the use of biophysical site index models (Mogren and Dolph, 1972; Klinka and Carter, 1990; Milner *et al*., 1996; Corona *et al*., 1998; Ung *et al*., 2001), non-linear models including soil and site attributes (Trasobares *et al*., 2004) or even process-based modelling (Landsberg *et al*., 2001, 2005). Statistical models provide evidence of the underlying relationships between site factors and growth, however they are limited to the range of the sampling data base and reflect the relations inserted in the statistical model employed.

Because such models require a relatively straightforward data collection system advanced decision support tools have recently been developed for application in British forestry. The Ecological Site Classification (ESC, Pyatt *et al*., 2001; Ray, 2001) is based on an extensive soil and vegetation survey conducted across Great Britain and produced estimates of soil nutrient and moisture regimes, using canonical correspondence and principal component analysis (Wilson *et al*., 2001, 2005). ESC feeds information to forest managers with regard to the suitability of species based on the ecological potential of specified sites, by assessing ground vegetation, soil characters and climatic information, such as accumulated temperature, moisture deficit, continentality and windiness. Additionally, it provides an estimate of the potential productivity of the selected species. Such tools can provide quick and efficient answers to questions related to site effects on tree growth.

However, an increased demand to understand the eco-physiological principles behind the growth dynamics of forest species and at the same time to explain tree growth with variables that are meaningful to ecologists and forest managers has led to the development of methodologies that allow predicting potential yield based on physiological principles of growth. For these reasons hybrid models have been implemented (Battaglia *et al*., 1999) or complex models have been simplified to adopt them to forest management needs. 3-PG belongs to this class of models (Landsberg and Waring, 1997). Furthermore, the latest development of the model, 3-PGN (see Chapter 4) includes a simple soil decomposition model to incorporate the main processes in the soil of a forest ecosystem. Although calibration procedures demand adequate amount of field data, its application can provide information both in terms of carbon storage and

timber yield. On the other hand, the multiple regression approach provides a quick and reliable analysis of the site factors important for stand growth.

This study is devoted to develop such a knowledge for Scots pine in Scotland, exploring the relationships between growth and site factors, to create the base for a future comparison between a purely statistical analysis and the use of an ecosystem model such as 3-PGN.

3.2 Materials and methods

3.2.1 Sampling sites selection

Forty five Scots pine stands were sampled between June and August of 2003 and 2004. These sites consist of monospecies, even-aged plantations with an average age of 50 years (Figure 3.1 and Table 3.1). The main selection criteria, except from age, included elevation (having a range from sea level to 507 m a.s.l.) and latitude (from $58^{\circ}\ 27'\ 34.2$" North to $54^{\circ}\ 54'\ 34.2$" North). Twelve sites belonged to the Forestry

Table 3.1: Summary of main climatic characteristics for the 45 sampling sites, including age (years), latitude (decimal degrees), longitude (decimal degrees), elevation (m), accumulated temperature ($\mathrm{Day-Degrees} > 5^{\circ}\mathrm{C}$) over the period of 1961-1990, continentality (unitless), DAMS windiness score (unitless) and moisture deficit (mm).

	Age	Lat	$Long$	$Elev$	AT	$Cont$	$DAMS$	MD
Mean	52.32	57.06	3.78	172.32	1119.01	5.14	13.12	94.42
SD	5.45	0.79	0.71	133.60	174.09	0.89	1.58	33.61
Minimum	39.00	54.91	2.60	1.00	697.31	3.57	9.40	-2.58
Maximum	67.00	58.46	5.54	507.00	1531.80	6.80	17.75	153.23

Commission's network of permanent sample plots (PSP) for which periodic mensuration data existed, twenty sites were part of Forest Research Level 1 monitoring plots, seven sites were part of the British Ecological Site Classification network (ESC, Wilson, 1998; Wilson *et al.*, 2001, 2005), while six plots were obtained by interrogating the Forest Enterprise database. The 45 sites extended between three main climate zones, i.e. cool moist, cool wet and warm moist according to ESC climatic descrip-

tions (Pyatt *et al.*, 2001). Soil types varied from sandy with a deep water table to deep peats (Pyatt *et al.*, 2001). Ground vegetation found in the majority of sites included mosses, bracken (*Pteridium aquilinum* (L.) Kuhn), wavy hair-grass (*Deschampsia flexuosa* L.), male fern (*Dryopteris filix-mas* (L.) Schott), wood-sorrel (*Oxalis acetosella* L.), heather (*Calluna vulgaris* (L.) Hull.) and billbery (*Vaccinium myrtillus* L.).

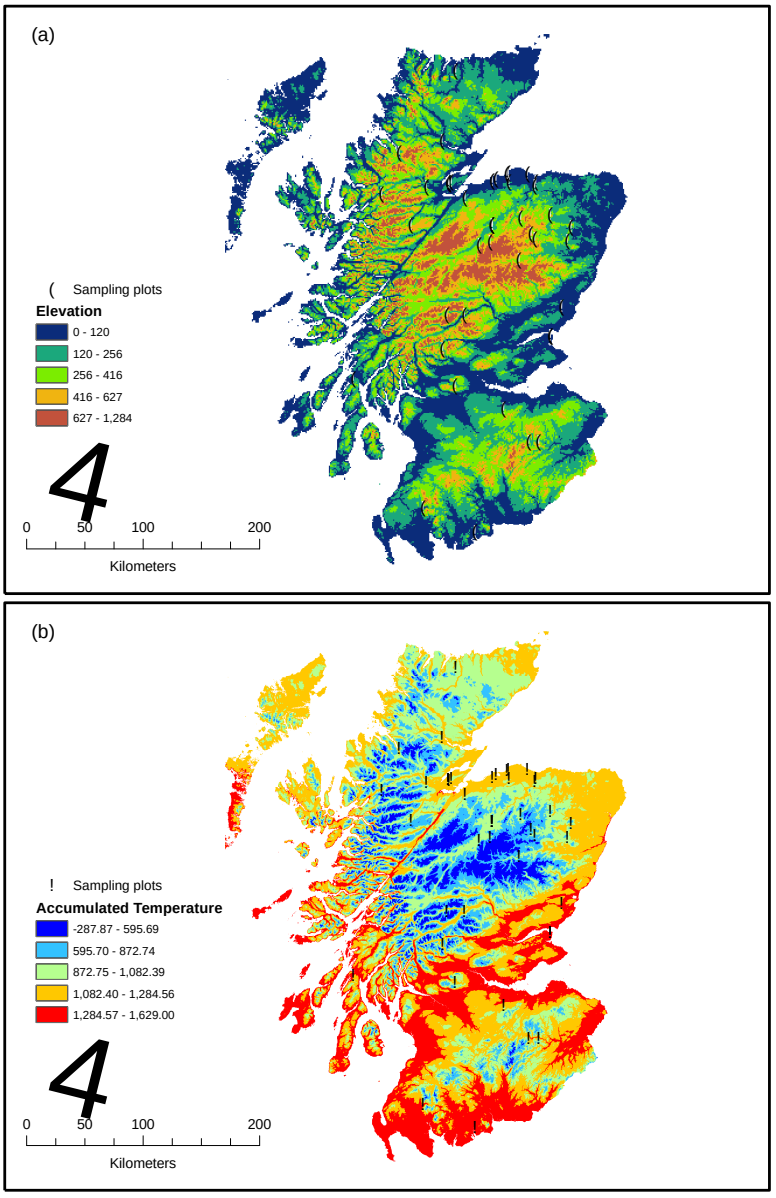

Figure 3.1: Geographical distribution of the 45 monoculture Scots pine stands visited during the summer period of 2003 and 2004, plotted on (a) an elevational (meters) and (b) on accumulated temperature ($\text{Day} - \text{Degrees} > 5^{\circ}\text{C}$) range.

3.2.2 Field measurements, soil and tree sampling

A circular plot of 0.1 ha was located randomly at each site and the location of the centre was recorded with a GPS. All living trees within the limits of the plot were counted and their diameter at breast height (D) was measured. Three dominant, healthy trees were identified and height was measured using a standard relascope. A tree core was also extracted from each tree and stored at cool temperatures ($< 5°\mathrm{C}$) waiting further analysis. The following soil sampling approach is described in details by Wilson *et al*. (2001) and Wilson *et al*. (2005). Here we provide a brief summary.

Three soil pits were excavated with dimensions of $60\,\mathrm{cm} \times 60\,\mathrm{cm} \times 30\,\mathrm{cm}$, one in the centre of the plot, one uphill and one downhill to account for variations due to potential differences in geology or effects of slope. Each pit was separated into two layers, one to 10 cm depth, the second from 10 to 30 cm depth and a soil sample of 1 kg was collected from each layer and stored in cool conditions awaiting laboratory analysis. The extracted soil from each pit was also weighted on location and a fraction was removed and stored separately under ambient conditions for the determination of bulk density. The central pit was further excavated down to 1 m, whenever possible. Soil profiles were examined and soil type, humus type, texture, depth and colour of each horizon were recorded using the methodology for the Ecological Site Classification (Pyatt *et al*., 2001). Ground vegetation, species composition and percentage cover for each species separately was recorded by placing five $2\,\mathrm{m} \times 2\,\mathrm{m}$ quadrants randomly within the plot.

3.2.3 Analysis and calculations

3.2.3.1 Soil samples

Soil samples were brought back to the lab and stored in a cold room ($< 5°\mathrm{C}$) until further analysis. The chilled samples were sieved to remove any stones above 2mm diameter and sub-sample were collected from each layer of each pit, and dried in the oven. A first 10 g sub-sample was extracted and used for estimating carbon and nitro-

gen stocks using an elemental C:N analyser. A further 10 g sub-sample was dissolved with 1 M potassium chloride and shaken for two hours. The filtered product was used to determine mineral components of available nitrogen, i.e. NO_3^- and NH_4^+, using colorimetric auto-analysis (Hawkes *et al.*, 1997).

Samples brought back for bulk density were dried under ambient condition for a couple of days, then sieved with a 2 mm sieve and oven-dried at 80-90°C for 48 hours and their weight was taken. Stones were weighed separately and bulk density was determined.

3.2.3.2 Tree cores and leaf area

Tree cores were soaked in a diazotized *o*-tolidine solution to stain and distinguish heartwood from sapwood by a colour reaction (Shain, 1967). The length of sapwood and radial growth of last five years was recorded using a digital calliper.

$$A_{SBLC} = 3.41689 \times A_{SBH} \times D^{-2/3} \tag{3.1}$$

$$L^* = 0.00303 \times A_{SBLC} \tag{3.2}$$

Leaf area (L^*, $\mathrm{m}^2\ \mathrm{m}^{-2}$) was estimated using two models developed by Mencuccini (2002, personal communication). The first model is relating sapwood area at breast height to sapwood area below the canopy (described by Equations 3.1) and a second model relating leaf area to sapwood area below the canopy (Equation 3.2), where A_{SBH} (mm^2) is the sapwood area at breast height as it was calculated from tree cores and A_{SBLC} (mm^2) is the sapwood area below canopy.

3.2.3.3 Volume and biomass

Volume (V, $\mathrm{m}^3\ \mathrm{ha}^{-1}$) was estimated using Forestry Commission's volume tariffs for the three measured trees using measured tree height and diameter at breast height and

scaled up using measured tree density. Aboveground (W_{AB}), stem (W_S), foliage (W_F) and root (W_R) biomass were calculated and scaled up for each plot, using pooled allometric equations developed for Scots pine from five studies across Europe (Ovington, 1957; Albrektson, 1980; Vanninen *et al*., 1996; Oleksyn *et al*., 1999; Xiao *et al*., 2003). For a description of the methodology employed to derive pooled allometric equations see Zianis and Mencuccini (2004). Biomass growth for the last five years and growth efficiency (GE), i.e., the biomass growth during the last five years divided by standing leaf area, was calculated using the developed allometric relations.

3.2.3.4 ESC output

Classes of soil texture, humus type, horizon depth, soil colour, stoniness, ground flora characterisation, percentage coverages and site location were used with the Ecological Site Classification to predict soil nutrient and moisture regime for each site. Other information extracted from ESC included species suitability, estimated yield increment (Y_{ESC}, $\mathrm{m^3\,ha^{-1}\,yr^{-1}}$) and predicted limiting factors for growth. Topographic information including slope ($\mathrm{degrees}$), aspects ($\mathrm{degrees}$) and elevation (m) were extracted from a 50 m resolution DEM provided by UK Ordnance Survey.

3.2.3.5 Climate

Climatic data employed in the analyses included mean monthly maximum and minimum temperatures ($^{\circ}\mathrm{C}$), mean monthly precipitation (mm), vapour pressure deficit (mBar), incoming solar radiation ($\mathrm{MJ\,m^{-2}\,day^{-1}}$), accumulated temperature ($\mathrm{Day-Degrees} > 5^{\mathrm{o}}\mathrm{C}$) over a 30 year period, moisture deficit (mm), continentality (a measure of seasonal variability of the climate, unitless), DAMS score (an indication of representing the amount of physiological or physical damage by wind exposure on a stand, unitless) and climate zone (an index of the type of climate). Values of temperature, precipitation and vapour pressure deficit were extracted from the 1 km spatial database developed by interpolating a data set obtained from the Climate Research Unit of the University of East Anglia (CRU), consisting of monthly averages for the

same variables for the period of 1961 - 1997 in a 10 km point grid. Solar radiation was estimated using a general algorithm by Nikolov and Zeller (1992) utilising inputs of monthly temperature, precipitation, relative humidity and applying corrections for topography by using latitude, elevation, slope and aspects. Accumulated temperatures, moisture deficit, DAMS score, continentality and climate zone were extracted from the ESC spatial climatic database. A summary of all climatic and soil characteristics of the forty five sample stands is given in Table 3.1.

Categorical variables such as soil moisture regime, soil nutrient regime and climate zone were transformed based on a ranking score assigned with a meaningful order. Ranking for soil moisture regime ranged from 1 for very wet to 8 for very dry sites. Soil nutrient regime was assigned 1 for very poor sites up to 6 for carbonated soils whereas climate zone was assigned from 1 for alpine to 7 for warm and dry climates (see also Table 3.2).

Table 3.2: Description and assigned scores of the categorical variables used in the analysis, including soil moisture regime (SMR), soil nutrient regime (SNR) and climate zone.

SMR	Score	SNR	Score	Climate Zone	Score
Very wet	1	Very poor	1	Alpine	1
Wet	2	Poor	2	Sub-Alpine	2
Very moist	3	Medium	3	Cool Wet	3
Moist	4	Rich	4	Cool Moist	4
Fresh	5	Very rich	5	Warm Wet	5
Slightly dry	6	Carbonate	6	Warm Moist	6
Moderate dry	7			Warm Dry	7
Very dry	8				

3.2.4 Statistical analysis

Before variables were used for any statistical analysis the assumption of normality was checked with a normality test using the Kolmogorov-Smirnov statistic and when necessary, appropriate transformation was applied. During the analysis a pairwise exclusion was employed causing however a significant decrease in the degrees of freedom. Impu-

tation of missing values was considered necessary using an expectation maximization algorithm, which estimated the expected value based on relations with other variables and then maximized the likelihood based on 100,000 iterations. Also a bivariate correlation test between independent variables was conducted to highlight any strong correlations which potentially could lead to significant collinearity effect in a multilinear regression model.

Table 3.3: Description of independent variables and their units used in this study.

Variable	Units	Description
Lat	decimal degrees	Latitude
$Long$	decimal degrees	Longitude
Asp	degrees	Aspects
$Slope$	degrees	Logarithm of slope
$Elev$	m	Square root of elevation
$Carbo$	$\mathrm{tC\ ha^{-1}}$	Soil carbon stocks
$Nitro$	$\mathrm{tN\ ha^{-1}}$	Soil nitrogen stocks
NO_3^-	$\mathrm{tC\ ha^{-1}}$	NO_3^- content
NH_4^+	$\mathrm{tC\ ha^{-1}}$	NH_4^+ content
$C{:}N$	-	C:N ratio
WC	-	Water content
AT	$\mathrm{Day-Degrees} > 5^{\mathrm{o}}\mathrm{C}$	Accumulated temperature
MD	mm	Moisture deficit
$Cont$	-	Continentality
$DAMS$	-	DAMS windiness score
CLZ	-	Climate zone
SMR	-	Soil moisture regime
SNR	-	Soil nutrients regime
Tx_{month}	°C	Mean monthly maximum temperature
Tn_{month}	°C	Mean monthly minimum temperature
$Precip_{month}$	mm	Monthly precipitation
$Solrad_{month}$	$\mathrm{MJ\ m^{-2}\ day^{-1}}$	Monthly incoming solar radiation
$Temp$	-	Principal component factor 1
$LackPrec$	-	Principal component factor 2
$SummerVPD$	-	Principal component factor 3
$WinterSR$	-	Principal component factor 4
$Wind$	-	Principal component factor 5
$LackSW$	-	Principal component factor 6
$Stocks$	-	Principal component factor 7
$Availability$	-	Principal component factor 8

To ensure such an effect is avoided, firstly a principal component analysis (PCA) was performed using all variables, including topography, soil carbon and nitrogen stocks,

nitrogen availability, mean monthly and ESC climatic variables, soil moisture and nutrient regime, and component factors were extracted. PCA also helped in reducing significantly the number of variables, which helped in the interpretation of the results. Dependent variables were then regressed against principal component factors using a multiple linear model and a stepwise selection procedure. Tables 3.3 and 3.4 give a description of all dependent and independent variables used in the analysis.

Table 3.4: Description of dependent variables and their units used in regression analysis. Logarithmic transformation was applied whenever appropriate to ensure the assumption of normality.

Variable	Units	Description
H	m	Tree height
$\log V$	$\log \mathrm{m}^3\ \mathrm{ha}^{-1}$	Logarithm of stand volume
$\log W_{AB}$	$\log \mathrm{tDM\ ha}^{-1}$	Logarithm of aboveground biomass
$\log V_{5m}$	$\log \mathrm{m}^3\ \mathrm{ha}^{-1}\ \mathrm{yr}^{-1}$	Logarithm of mean volume increment over the last 5 year
$\log W_{AB_{5m}}$	$\log \mathrm{tDM\ ha}^{-1}\ \mathrm{yr}^{-1}$	Logarithm of aboveground mean biomass growth over the last 5 year
$\log L^*$	$\log \mathrm{m}^2\ \mathrm{m}^{-2}$	Logarithm of leaf area index
GE	$\mathrm{kg\ m}^{-2}$	Tree level growth efficiency
GYC	$\mathrm{m}^3\ \mathrm{ha}^{-1}\ \mathrm{yr}^{-1}$	General Yield Class

3.3 Results

3.3.1 Pooled allometric equations

Table 3.5: Parameters, coefficient of determination and standard error of estimate for the linear allometric model $\ln Y = \ln a + b \ln D$ used to determine above ground, stem, foliage and root biomass.

Variable	$\ln a$	b	Adj. R^2	SEE	n	P
$\ln W_{AB}$	-2.647	2.504	0.990	0.18697	70	< 0.01
$\ln W_S$	-2.861	2.457	0.975	0.29897	70	< 0.01
$\ln W_F$	-3.609	1.804	0.842	0.59192	70	< 0.01
$\ln W_R$	-3.126	2.052	0.931	0.45149	46	< 0.01

Table 3.5 gives the coefficients, coefficients of determination, standard error of estimate and significance level for the pooled allometric regression models while Figures 3.2 show the models in arithmetic and logarithmic scale for aboveground, stem, foliage and root biomass.

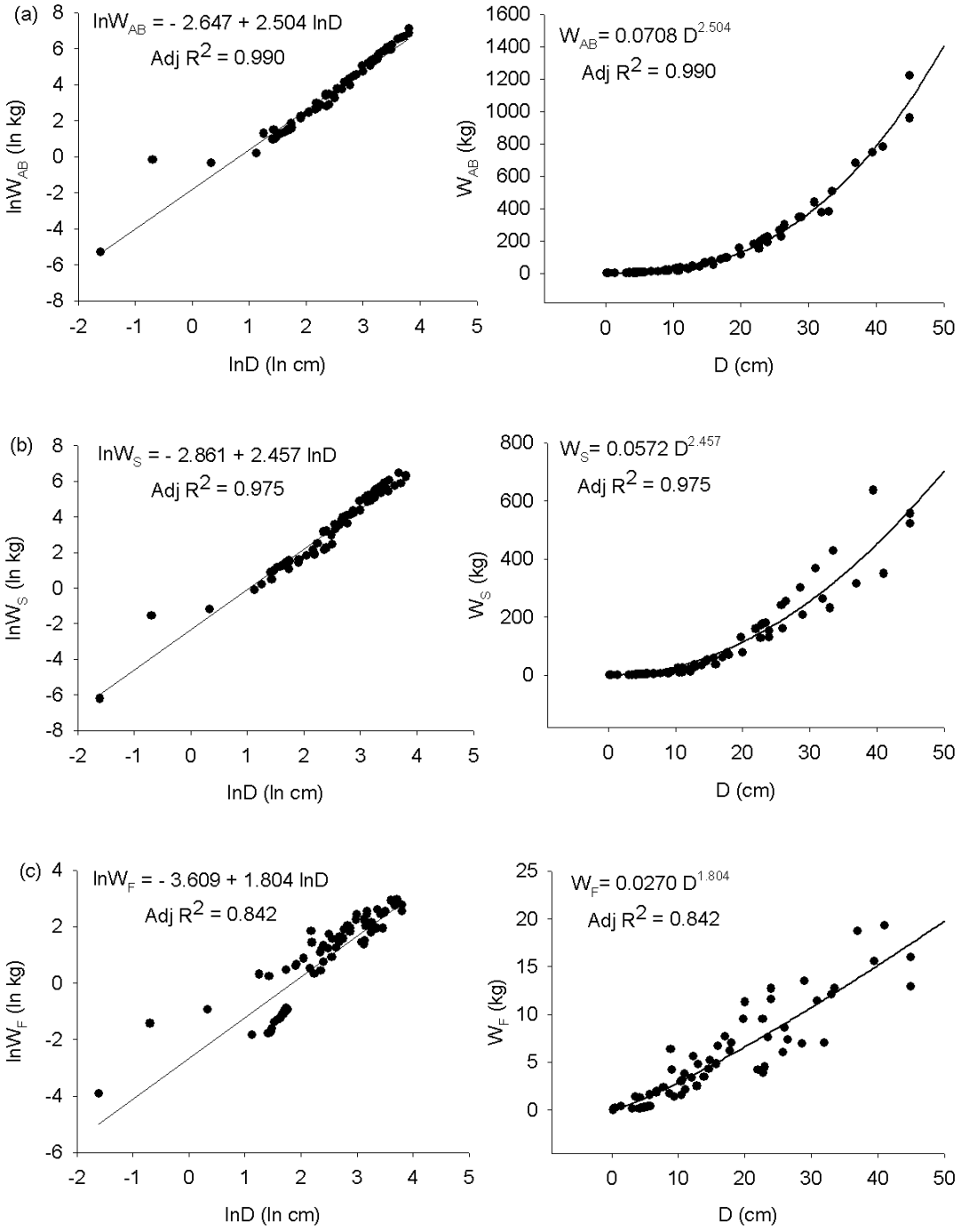

Figure 3.2: Pooled regression allometric relations in logarithmic and arithmetic scale for (a) above ground (kg), (b) stem (kg), (c) foliage (kg) and (d) root biomass (kg) for Scots pine.

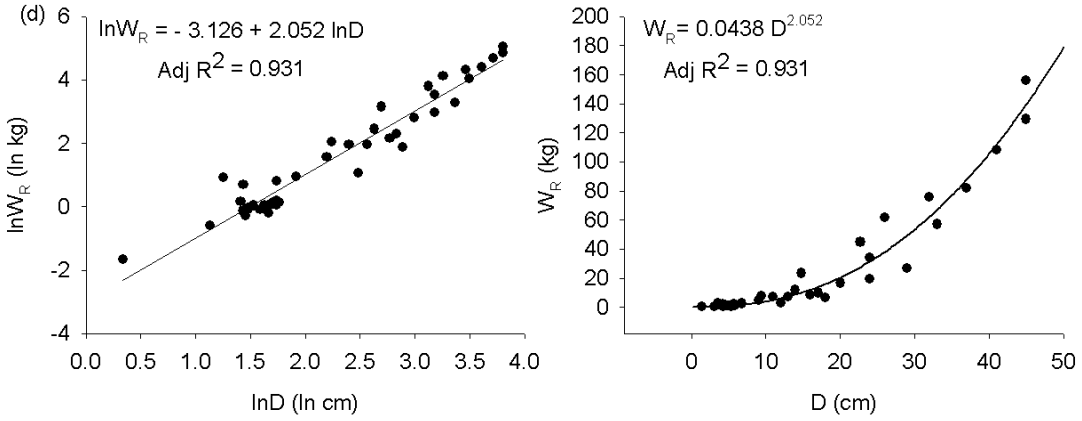

Figure 3.2: *Continued*

Regression analysis gave four highly significant models with the highest coefficient of determination for aboveground biomass ($\mathrm{R}^2 = 0.99$) and the lowest for foliage biomass. Although the model for foliage biomass explained 84% of the variance, there is a part of the variance which remained unexplained (Figure 3.2). The range of coefficient a is between -2.6 and -3.6 whereas the coefficient b is between 1.8 and 2.5.

3.3.2 Correlation analysis

Pearson correlation coefficients between independent variables are presented in Table 3.6. Monthly inputs of temperature, precipitation, vapour pressure deficit and solar radiation were excluded from this analysis as interactions with climate are sufficiently represented by ESC variable.

Highly significant positive relations exist between elevation and slope, nitrogen stocks and elevation, carbon and nitrogen stocks and available NO_3^- and NH_4^+. Also positively correlated are soil water content and elevation, C:N ratio and latitude, moisture deficit with accumulated temperature and climate zone. Strong negative correlations also exist between accumulated temperature and elevation, slope and carbon stocks, and between moisture deficit with slope and aspects. Finally $DAMS$ score is significantly correlated with elevation, accumulated temperature, climate zone and soil carbon stocks.

Table 3.6: Correlation between independent variables used in principal component analysis.

	Lat	$Long$	$Elev$	Asp	$Slope$	$Nitro$	$Carbo$	$C{:}N$	WC	NO_3^-	NH_4^+	AT	CLZ	$Cont$	$DAMS$	MD
Lat	1	0.102	-0.165	0.110	-0.102	-0.179	0.063	0.433**	-0.089	0.082	0.226	-0.278	-0.155	-0.587**	-0.121	0.013
$Long$		1	-0.170	0.262	0.197	-0.068	-0.038	0.074	-0.037	-0.075	-0.109	0.135	0.013	-0.618**	0.127	-0.118
$Elev$			1	0.240	0.561**	0.462**	0.376*	-0.146	0.409**	-0.047	-0.106	-0.893**	-0.785**	0.674**	0.586**	-0.941**
Asp				1	0.077	0.360*	0.325*	-0.100	0.131	-0.296	-0.272	-0.247	-0.375*	-0.058	0.169	-0.306*
$Slope$					1	0.296	0.171	-0.222	0.336*	-0.113	-0.152	-0.553**	-0.505**	0.261	0.378*	-0.650**
$Nitro$						1	0.843**	-0.267	0.215	-0.185	-0.195	-0.376*	-0.355*	0.343*	0.287	-0.432**
$Carbo$							1	0.242	0.111	-0.184	-0.081	-0.396**	-0.353*	0.177	0.330*	-0.398**
$C{:}N$								1	-0.146	0.114	0.274	-0.050	-0.016	-0.311*	0.115	0.043
WC									1	-0.011	-0.241	-0.372*	-0.348*	0.276	0.144	-0.399**
NO_3^-										1	0.830**	0.029	0.041	0.027	-0.151	0.084
NH_4^+											1	0.022	0.030	-0.101	-0.003	0.129
AT												1	0.831**	-0.404**	-0.531**	0.912**
CLZ													1	-0.328*	-0.603**	0.811**
$Cont$														1	0.160	-0.432**
$DAMS$															1	-0.646**
MD																1

** Significant at $P < 0.01$, * Significant at $P < 0.05$

Finally, continentality is highly significantly correlated with latitude and longitude, elevation and accumulated temperature, whereas there is a lower significant correlation with nitrogen stocks, C:N ratio and climate zone. The correlation analysis showed that data should be handled with extreme caution as an attempt to interpret a regression model using those highly intercorrelated independent variables could cause problems.

Table 3.7: Percentage of variance explained by the eight principal component factors with eigenvalues greater than one.

Component	Total	% of Variance	Cumulative %
1	35.62	45.67	45.67
2	16.39	21.01	66.68
3	6.87	8.81	75.49
4	5.99	7.68	83.17
5	2.93	3.76	86.93
6	2.11	2.70	89.63
7	1.39	1.78	91.41
8	1.31	1.68	93.09

3.3.3 Principal Component Analysis

Principal component analysis gave eight major factors with eigenvalues above the threshold of 1 (Table 3.7), explaining in total 93.09% of the variance. The first component explained 45.67% of the variance and includes the positive effect of minimum monthly temperature (mainly winter) with winter maximum temperatures and a negative effect of elevation with continentality and soil nutrient regime (Figure 3.3, page 75). The factor was denoted as temperature effect and more specifically minimum temperatures ($Temp$) but with a clear indication of an elevation-temperature interaction. The second factor on the other hand, explains 21.01% of the variance and 66.68% together with factor 1. The factor is strongly influenced by monthly precipitation and so it was denoted as lack of precipitation effect ($LackPrec$) due to its negative contribution but with a clear indication of west-east because of a significant contribution from longitude. The fact that late spring - early summer incoming solar radiation has a positive contribution the factor then could be considered as a late spring - early summer lack of precipitation.

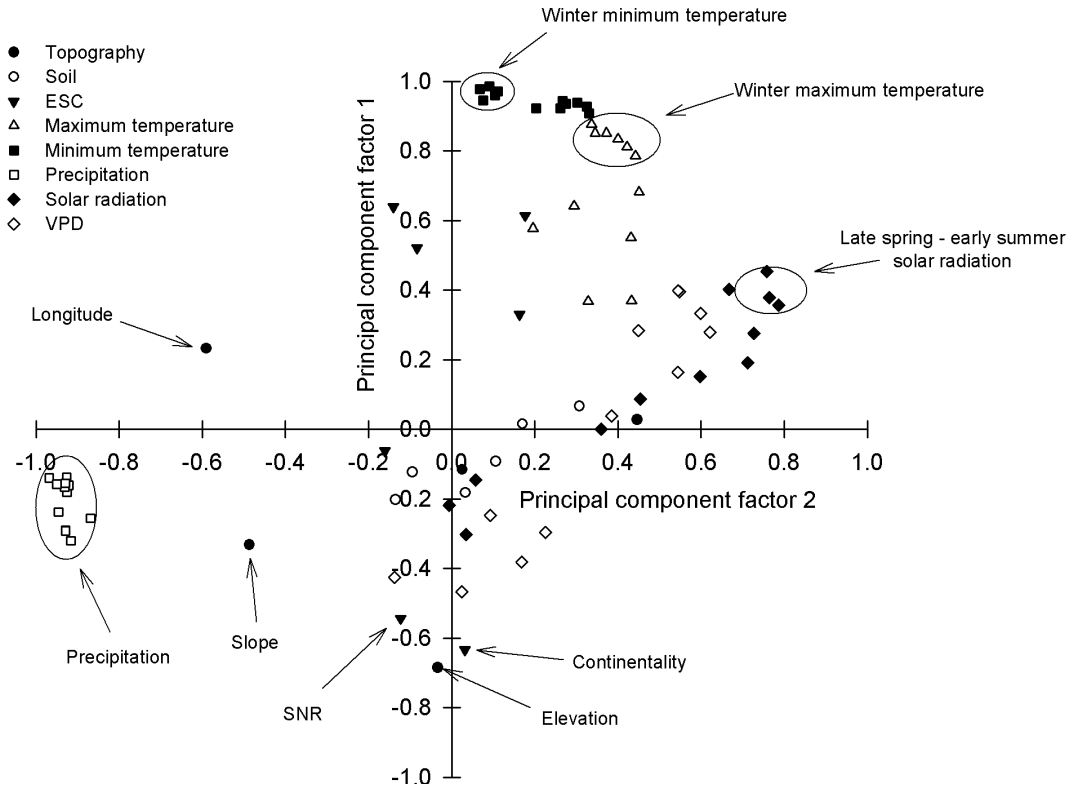

Figure 3.3: Component loadings for factors 1 and 2. Factor 1 is mainly influenced by monthly minimum winter temperatures and winter maximum temperatures, elevation, continentality and SNR, representing either warm, low elevation sites with low soil nutrient status or high elevation sites with lower temperature and higher soil nutrient status. The factor however was denoted as temperature. Factor 2 on the other hand, is mainly influenced from mean monthly precipitation, late spring - early summer solar radiation and longitude, indicating sites with high precipitation but low sunshine during summer time or vice versa (see also Figure 3.7). The factor could be considered also as an indication between east-west however, for the analysis it was denoted as lack of precipitation.

Although the interpretation of factor 3 becomes a bit more difficult (Figure 3.4, page 76) there is a good agreement with the interpretation of the second factor. Factor 3 explains 8.81% of the variance and 75.49% with factors 2 and 3. It was denoted as effect of summer vapour presure deficit ($SummerVPD$) but again with a clear indication between east and west. Late spring and summer values are the main contributors, which again suggests that for eastern sites there is a considerable lack of precipitation. Factor 4 explains 7.68% of the variance and 83.17% in total. The factor was denoted as winter solar radiation ($WinterSR$) because of the significant contribution of solar radiation values during the winter months. Latitude however, is also very significant contributor suggesting that the factor mainly represents southern, less cloudy sites during the winter months which they appear to have a more continental climate.

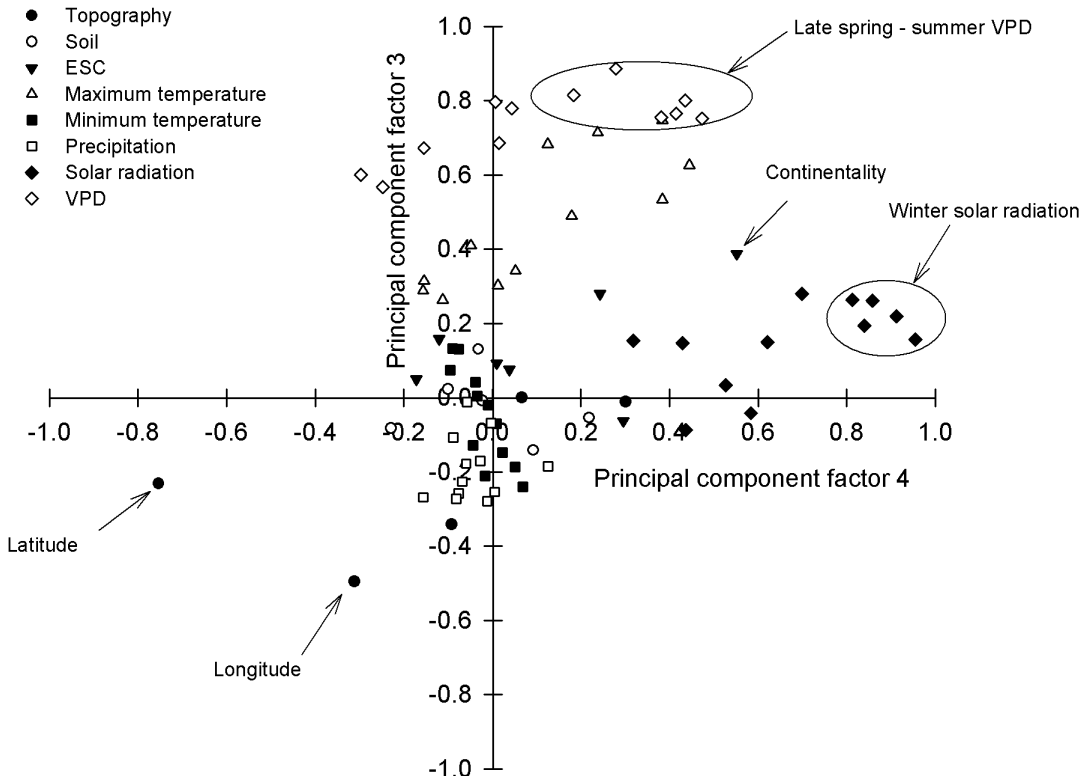

Figure 3.4: Component loadings for factors 3 and 4. Factor 3 is influenced by late spring - summer VPD and longitude showing similarly to factor 2 that western sites are more humid. The factor was denoted as VPD. Factor 4 consists mainly winter solar radiation and latitude, suggesting that northern sites are cloudier during winter period and so it was denoted as winter solar radiation (see also Figure 3.7).

The interpretation of factor 5 is a more straightforward (Figure 3.5, page 77). There is a strong effect of the $DAMS$ windiness score, explaining 3.76% of the variance and 86.93% in total. Thus the factor was denoted as wind effect ($Wind$). Other ESC climatic variables such as accumulated temperature, moisture deficit and climate zone are also significant contributors with climate zone being the strongest. The elevation and slope comes to complete the interpretation of the factor that high altitude, deep slope sites are more exposed to gale forces which significanlty cools the atmosphere and brings more rainfall, that is western, cool wet type of climate. Factor 6 was denoted as lack of soil water ($LackSW$) because of the main negative effect of soil water content. The contribution of C:N ratio, SMR and SNR is also significant sugessting that dry sites have a poor nutritional status and low carbon content.

Finally, factors 7 and 8 (Figure 3.6, page 78) although their contribution to the total

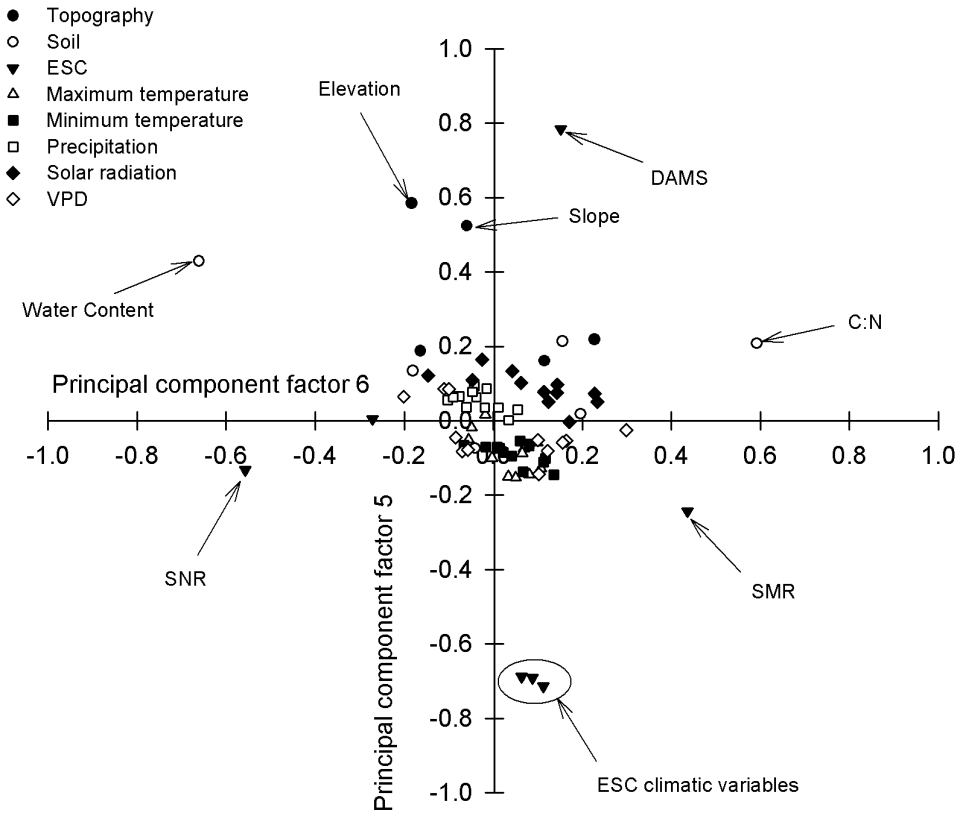

Figure 3.5: Component loadings for factors 5 and 6. Factor 5 appears to be influences mainly from ESC climatic variables such as $DAMS$, AT, $Cont$, and CLZ with elevation and slope also included. The factor shows that high elevation sites placed on slopes are more wind exposed but with also lower temperatures and more rain, thus cool and wet sites. On the other hand, factor 8 shows large influence from soil water content, C:N, soil moisture regime and soil nutrient regime indicating dry and low in nutrients sites.

variance is very small with 1.78 and 1.68% respectively they appear to be signficiant (eigenvalue > 1). Factor 7 was denoted as soil carbon and nitrogen stocks ($Stocks$) as those are the most significant contributors. Aspects also appear to have an effect which seems to suggests that soil on western exposed slopes contain more carbon and nitrogen. On the other hand, factor 8 was denoted clearly as nitrogen availability ($Availability$) as the major contributors are ammonium and nitrate contents.

3.3.4 Multiple regression analysis

A summary of the multiple linear regression coefficients and coefficients of determination are presented in in Table 3.8. The highest proportion of variance explained was

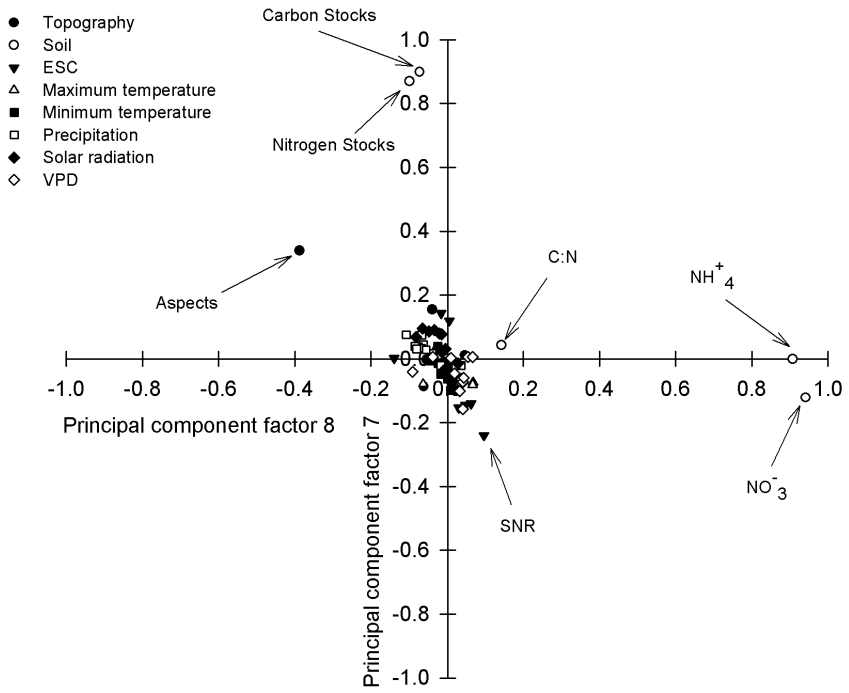

Figure 3.6: Component loadings for factors 7 and 8. Factor 7 clearly represents soil carbon and nitrogen stocks whereas factor 8 represents the effect of ammonium and nitrate, thus they were denoted stocks and availability respectively.

found for tree height with R^2 of 0.331. Three major component factor were significantly related with tree heigh ($P < 0.01$). Lack of precipitation was negatively related to height, wind was found to be also negatively related while there was a significant positive relation with soil stocks.

Table 3.8: Coefficient values, coefficients of determination and significance level for the multiple regression analysis. Symbols for the dependent and independent variables are given in Tables 3.4 and 3.3 respectively.

	Constant	$Temp$	$LackPrec$	$WinterSR$	$Wind$	$Stocks$	R^2	P
H	19.346	—	-1.348	—	-0.952	0.851	0.331	< 0.01
GYC	10.500	—	-1.135	0.875	—	—	0.305	< 0.01
$\ln V$	2.567	0.057	-0.069	—	—	—	0.266	< 0.05
$\ln W_{AB}$	2.349	0.051	-0.070	—	—	—	0.256	< 0.05
$\ln L^*$	0.409	0.059	—	—	—	—	0.104	< 0.05
GE	1.193	0.107	—	—	—	—	0.099	< 0.05

The model for general yield class gave an R^2 of 0.305 with two significant predictors ($P < 0.01$), lack of precipitation and winter solar radiation. Lack of precipitation again appears to be negatively related with yield class whereas winter solar radiation has a

positive effect. The logarithm of standing volume on the other hand was significantly related to temperature and lack of precipitation factors with an R^2 of 0.266. Temperature factor appears to be positively related with stand volume whereas lack of precipitation appears again to have a negative effect. Furthermore, aboveground biomass although appear to have the same predictors R^2 was lower with 0.256 ($P < 0.05$). Leaf area index and growth efficiency also showed significant but not strong relations with R^2 of 0.104 and 0.099 respectively ($P < 0.05$). For both variables there was a significant positive relation with temperature component factor.

Lack of precipitation appears in four out of six regression model as a very significant factor whereas factors for vapour pressure deficit, lack of soil water, and availability do not appear in any model.

3.4 Discussion

Principal regression analysis resulted in six significant models. Height was found to be significantly related with factor 2 ($LackPrecip$), factor 5 ($Wind$) and factor 7 ($Stocks$). A negative relation with factor 2 indicates a positive effect of precipitation on height development. However, strong is the contribution of longitude to the factor which suggests that there is a strong west-east difference in height of Scots pine stands across Scotland with the western stand have the potential for greater development. Significant to the factor is also the contribution of late spring - early summer incoming solar radiation, which is negatively related with longitude suggesting that eastern stands during summer receive greater amounts of sunshine (see also Figure 3.7). Combined the effect of spring - summer solar radiation and the lack of precipitation suggests that there is a limitation on height development by late spring - early summer drought on the east parts of Scotland. As solar radiation starts to increase, soil water availability on the well drained soils becomes limited as there is no continuous input of precipitation, leading to stomata closure. Summer precipitation will eventually cause the stomata to re-open, however a limitation on photosynthesis during the early stages of the growing season would have resulted in growth reduction.

Height was also found to be significantly related with principal component factor for wind. High elevation stands on steep slopes appear to be more exposed to oceanic winds which limits height development and reducing productivity by stressing tree and forcing carbon allocation to either stem or roots to enhance stability. Lundqvist and Valinger (1996) found that Scots pine trees are capable of retaining information about mechanical stress on their stems during winter and respond to that during the following growing season by changing allocation patterns accordingly. Atlantic wind currents, which usually are stronger on the west of Scotland, will substantially decrease air temperature and bring a significant amount of clouds reducing the annual incoming solar radiation and increase atmospheric and soil moisture. Similar observations were reported for Scots pine in Finland, where western coastal line have lower height development than the inner parts of the country (Karlsson, 2000).

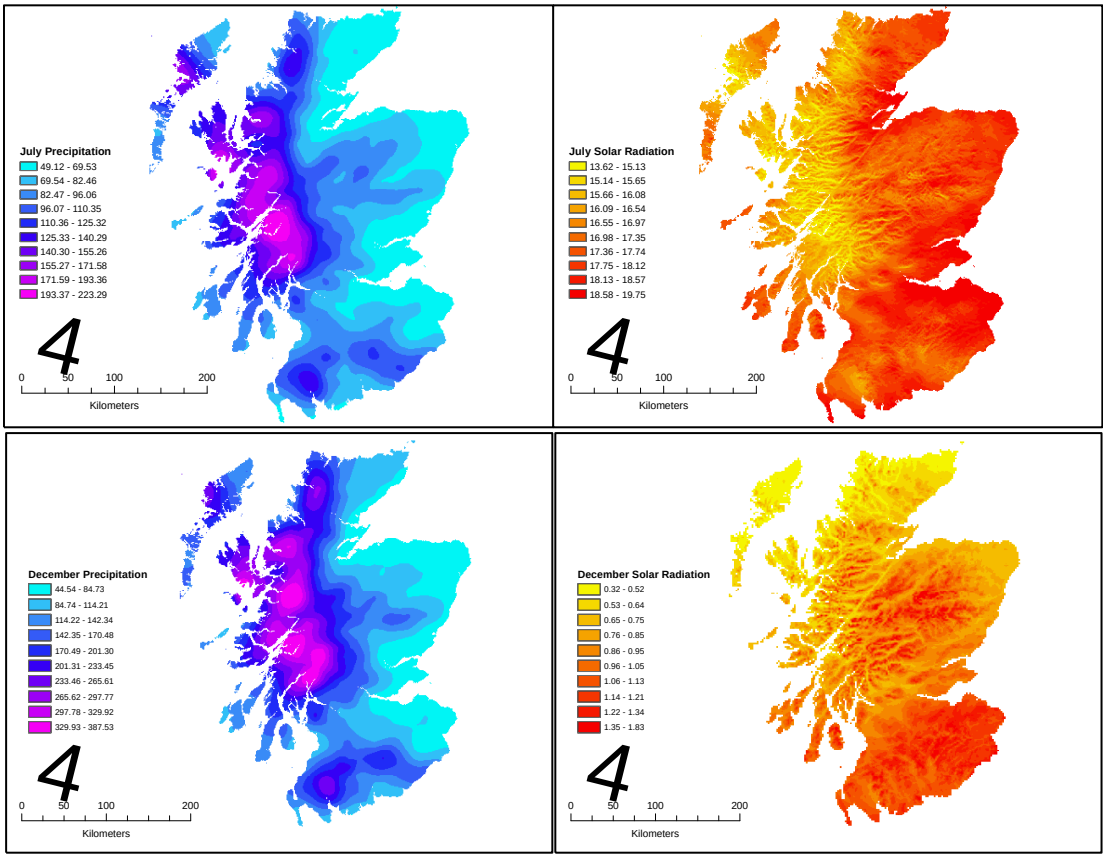

Figure 3.7: Spatial surfaces of July's and December's precipitation (mm) and incoming solar radiation (MJ m^{-2} day^{-1}) averages over the period between 1961 and 1990. During summer western Scotland appears to be more cloudy with greater precipitation than the east. During winter on the other hand, the north west of Scotland becomes very cloudy however, the heavy load of precipitation is concentrated on the west central belt with the southern regions receiving more sunshine.

Our model also showed a strong positive relationship with the factor for soil carbon and nitrogen stocks indicating an increase in height with an increase in stocks. Although that could not be translated as a direct effect of soil fertility on growth as soil nitrogen stock does not consist nitrogen in an available form for trees, such a relationship is very difficult to explain. A logical hypothesis however, would be that as trees grow taller, litter is increased either due to senescence or wind damage which will potentially lead to an increase to stocks. Nevertheless, there are not sufficient data to support such a hypothesis.

General yield class was also found to be positively related with precipitation suggesting once again that summer drought on eastern parts of having a great significance on development of timber growth and height. Furthermore, factor 4 was found to have an effect on yield class of Scots pine. The model showed that an increase in sunshine during the winter months will have an impact on timber growth which suggests that Scots pine is a species which is able to photosynthesise when ever appropriate conditions are found even during winter. However, our data suggest that this phenomenon is concentrated only on certain areas of Scotland and more specific on south-eastern parts. Continentality, latitude and longitude are the variables indicating such a topographic variation in winter photosynthesis. Latitude is clearly a strong contributor and although longitude appears to have some effect, continentality is also very strong. Continentality is used by ESC as indicator of climate and how close it is to a European continental type of climate. High values of continentality normally appear on the south-east with a clear orientation to continental Europe. The fact that continentality appears slightly strong contributor to the factor could indicate only one thing, the topographic distribution of the phenomenon of winter photosynthesis (see also Figure 3.7).

Apparently photosynthetic activity of Scots pine during winter is not something unknown for UK populations. Fry and Phillips (1977) showed a considerable amount of dry matter accumulation during winter months were temperatures are above zero. It was found that Scots pine potentially could respond to quite wide fluctuations in daily temperatures. Rutter (1957) also showed that solar radiation during early and late winter is sufficient to enhance photosynthetic activity and dry mass formulation. Neilson

and Jarvis (1972) showed that physiological processes of adaptation took place in Sitka spruce, allowing photosynthesis to take place when exposed under temperatures close to zero which completely agrees with the findings by Turner and Jarvis (1975) and is also supported by data from Fry and Phillips (1977) for Scots pine.

The significance of late spring - early summer drought was also present for volume and aboveground biomass. Scots pine stands on the east of Scotland in their vast majority are growing on well drained soils such as brown earths, podzols and sandy soils with deep water tables (Figure 3.8). Monthly variation of precipitation for eastern stands showed that during April the lowest amount of rainfall occurs with approximately 40 mm of rain, whereas for western stands the period of low rainfall extends over the summer. However, western stands remain cloudy through out the period (Figure 3.7) reducing evaporation due to increased temperatures.

Drought during summer is a phenomenon that is known to have a limiting effect on growth and establishment of Scots pine in Mediterranean regions (Castro *et al*., 2005), however it is something that has not been observed in high latitude regions and in particular Scotland, where normally annual precipitation ranges from 630 to 2500 mm with an average of 1000 mm a year and half occurring during the six months of spring and summer. Temperatures however, have been increased approximately 0.5 $^{\circ}\mathrm{C}$ over the last 100 years in north hemisphere (Huang *et al*., 2000), which could have resulted into drought effects for stands on the east of Scotland, as this is the region where a low $\mathrm{CO_2}$ emission climate change scenario for the UK is expected to have a 30% reduction in summer precipitation (UKCIP02, Hulme *et al*., 2002).

A significant drought effect in photosynthetic capacity was also found by Fry and Phillips (1977) who showed that during April and May of 1973 evergreen trees were subjected to possible water stress, without however excluding the possibility of such a phenomenon to be responsible due to hormonal changes in the photosynthetic activity.

Temperature factor appear for the first time in the stand volume regression model to be significant highlighting a relation between temperature and stand volume or above-ground biomass. Having a better look into the temperature factor we see that mini-

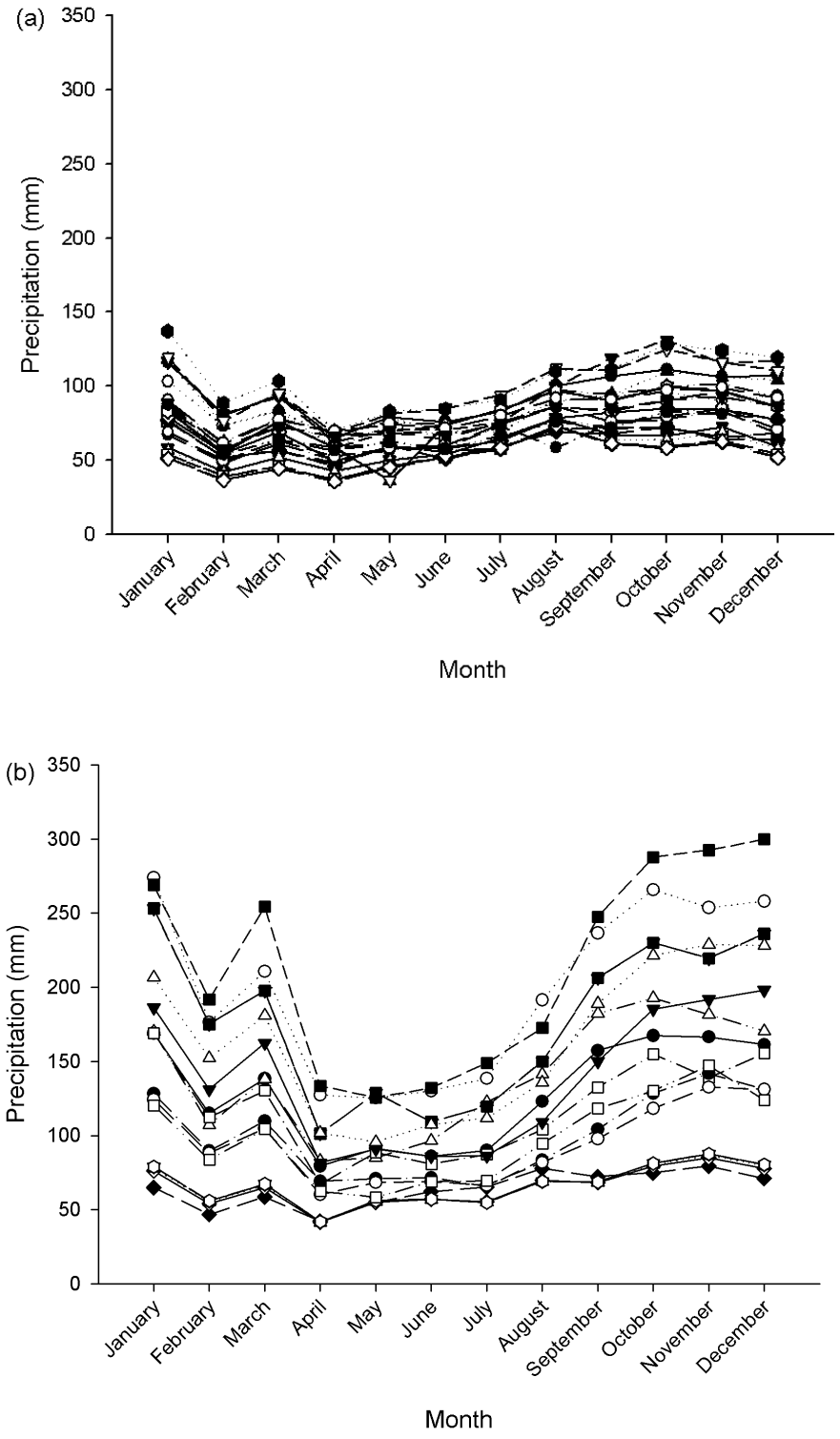

Figure 3.8: Monthly variation of precipitation (mm) for (a) plots on the east of Scotland, (b) on the west and a map of soil type for eastern plots.

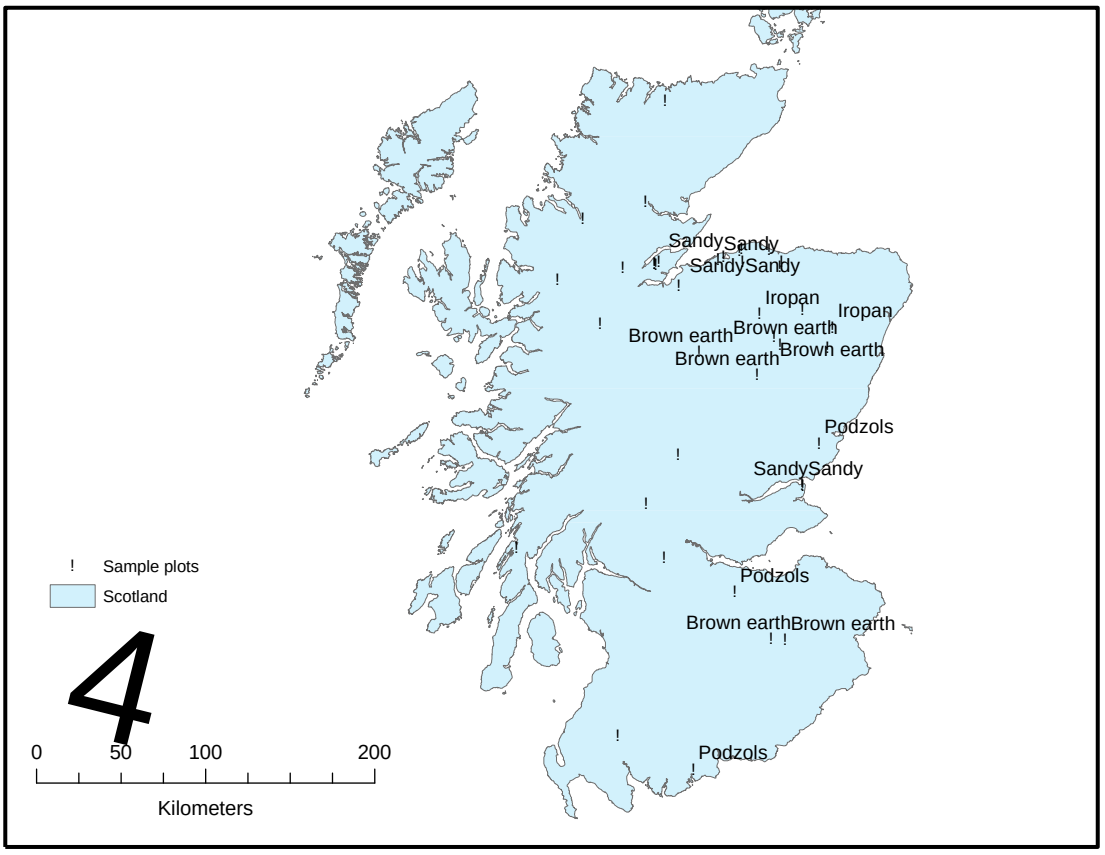

Figure 3.9: Soil types for the sampling plots on the east of Scotland

mum and maximum winter temperatures are between the most significant values for stand volume and aboveground biomass development, suggesting that rising temperature during winter period there is sufficient photosynthetic activity, which is consistent with the increase of yield class with incoming solar radiation for the same period. It also suggests that winter frost could potentially limit growth. Furthermore, the model highlighted the negative relation of biomass and volume with increasing elevation. Relation between aboveground net primary productivity and elevation was found by Zianis and Mencuccini (2005) for beech trees in Greece, suggesting a variety of reasons including a decrease in the length of growing season, lower temperature or a decline of foliar nutrient concentration.

The model also showed that stand volume and aboveground biomass increase when soil nutrient regime becomes low, that is, when relatively poor nutrient soils. That means, Scots pine grows sufficiently well on poor nutrient soils with low elevation but high enough temperatures during winter to support photosynthesis. Although those

sites growth is usually limited by summer drought, the development of Scots pine is sufficiently good. This agrees with Brown and Nisbet (1894) who describe Scots pine as a species that grows best *"on gravelly loam resting upon a dry stratum of rotten rock, but excellent timber may also be formed upon a dry sandy loam"*. He also supports that Scots pine is found in almost every variety of land, but the dry light sandy or gravelly loams appear to be the best soils for growth of larger crops, something which was also observed during the field sampling. Scots pine was found to grow on east coastal sandy soils with deep water table, something which supports Brown and Nisbet (1894) findings that the development of the root system in such soils can be very deep, reaching for lower soil layers which usually retain moisture.

Finally, a significant relationship was found between leaf area index and growth efficiency with temperature factor respectively. Leaf area appears to be greater for those low elevation, poor nutrient but sufficiently warm sites. Trees in warmer sites will increase leaf development as there would be a strong need to support an enhanced photosynthetic activity due to increased solar radiation and temperatures. Growth efficiency on the other hand, although it does not appear to be strongly related with temperature factor it suggests that warmer, low elevation sites during winter produce more biomass per unit of leaf area than high elevation stands. Zianis and Mencuccini (2005) also supports our findings who found similar trends of leaf area and growth efficiency with elevation.

The positive relationship between temperature and growth is well established for Scots pine (Luomala *et al*., 2003). Higher temperatures cause the stomata to open and allow greater CO_2 uptake. Vapour pressure deficit is also known to affect photosynthesis by causing stomata closure (Beadle *et al*., 1985). Many previous studies identified the effect of temperature and rainfall on Scots pine growth either in Europe (Corona *et al*., 1998; Fries *et al*., 1998; Tegelmark, 1999) or Scotland (Cook *et al*., 1977; White, 1982a,b; Tyler *et al*., 1996). The importance of temperature and rainfall on site index and thus height development is also well documented for many species (Klinka and Carter, 1990; Milner *et al*., 1996; Corona *et al*., 1998). Temperature may also affect the quality of timber produced, with high temperatures associated with increased stem

wood density but also increasing number and size of branches. Temperature and site fertility are also reported to affect growth of Scots pine by Fries *et al.* (1998). On the other hand White (1982a,b) reports that Scots pine growth in Great Britain is mainly associated with incoming solar radiation, soil texture and soil moisture content.

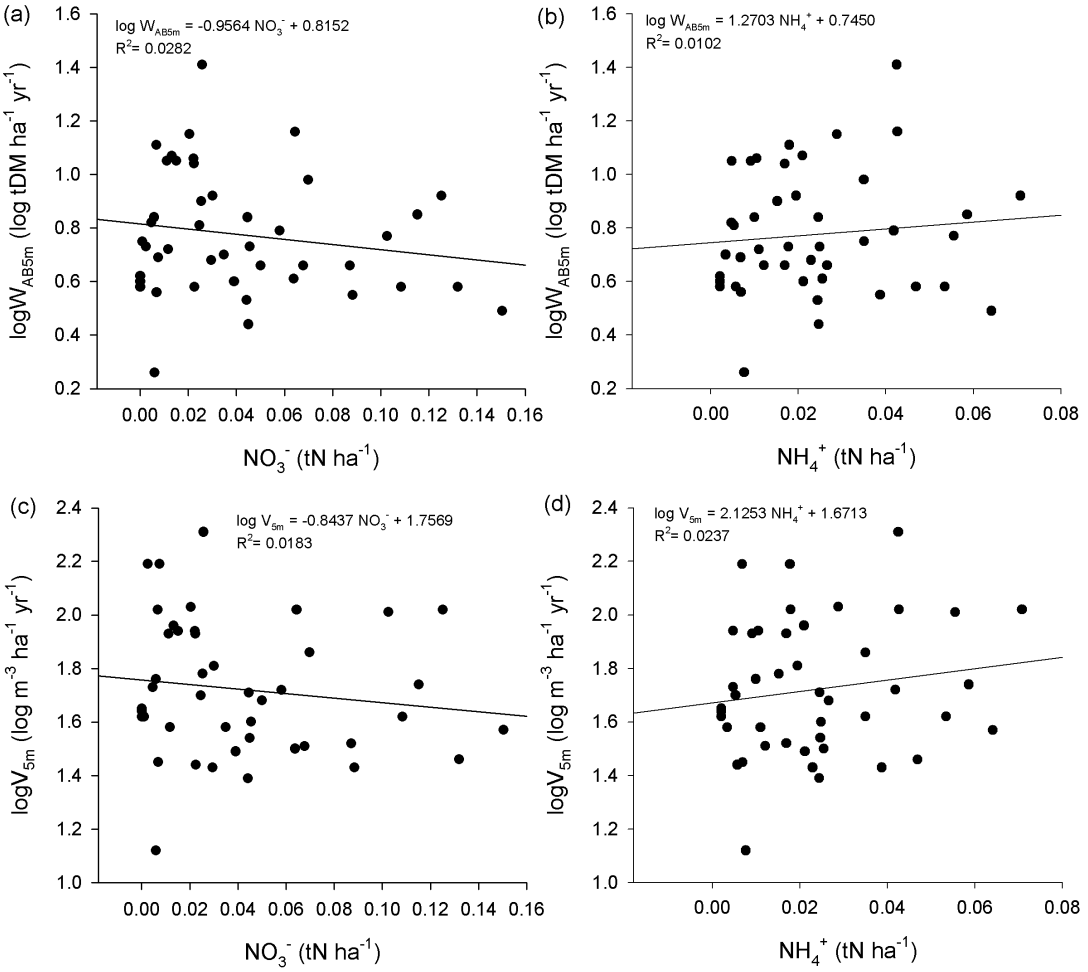

Figure 3.10: Trends of the logarithm of increment over the last five years for (a) mean aboveground biomass with available soil nitrate (NO_3^-, $\mathrm{tN\ ha^{-1}}$) and (b) with available soil ammonium (NH_4^+, $\mathrm{tN\ ha^{-1}}$) and (c) stand volume with available soil nitrate and (d) available soil ammonium.

Although our regression models showed that standing biomass and timber is higher on poor nutrient soils (Figure 3.3 and Table 3.8), there was no clear indication of the effect of nutrients on growth. When plotting mean volume and aboveground biomass increments over the last five years against NO_3^- and NH_4^+ content (Figure 3.10) no significant relationship was found although a weak trend was recognised. Nevertheless, the general trend was that nitrate content could have a limiting effect on both volume and

biomass growth with ammonium having the opposite effect. The preference of Scots pine for NH_4^+ could be explained by the acidity of the soils, as increased NO_3^- content will increase alkalinity, conditions not favourable for growth. Vollbrecht and Kasemir (1992) showed that sites of Scots pine, root systems were significantly increased with increased ammonium supply, changing also the morphology of the roots. Moreover, Öhlund and Näsholm (2004) showed that the uptake rate of ammonium for Scots pine seedlings was seven to eight times greater than the uptake of nitrate although it appears that they can take more than they can incorporate into proteins, resulting into storage of nitrogen in different forms (Flaig and Mohr, 1992). Finally, ammonium is the form of mineral nitrogen preferred by the ectomycorrhiza commonly found in the root system of pines (Ingacio Rangel-Castro *et al.*, 2002). The significance of other soil chemical elements and of soil acidity on Scots pine was also illustrated by Holmgren (1994) and White (1982a,b). The importance of soil chemistry was also well documented by several other studies with regard to either height growth (White, 1982a,b; Karlsson, 2000) or site index (Mogren and Dolph, 1972; Klinka and Carter, 1990; Holmgren, 1994; Milner *et al.*, 1996; Elfving and Kiviste, 1997; Corona *et al.*, 1998; Bravo and Montero, 2001).

From the application of Ecological Site Classification we were also able to extract information about species suitability for the 45 sampling sites and a prediction of expected yield production (Y_{ESC}). Figure 3.11 shows the frequency distribution of yield class produced by our principal regression model, observed general yield class and the predictions by ESC. Mean observed yield class for Scots pine was 10.5 $\mathrm{m}^3\,\mathrm{ha}^{-1}\,\mathrm{yr}^{-1}$ whereas mean Y_{ESC} was 7.33 $\mathrm{m}^3\,\mathrm{ha}^{-1}\,\mathrm{yr}^{-1}$. From Figure 3.11 it is obvious that ESC gives the most pessimistic prediction of yield class whereas our regression model with a mean of 10 $\mathrm{m}^3\,\mathrm{ha}^{-1}\,\mathrm{yr}^{-1}$ gives very close predictions. However, the variance of both the PCA model and ESC is much smaller than the observed. This larger variance gives the impression that growth of Scots pine is very different amongst sites, however such large variation must be due to the fact that no adjustments were made in the estimation of the localised yield class. On the other hand, it could be the case that this discrepancy in the variance between the two models and observation is due to effect of drought which both were able to capture, whereas in the estimation of general yield class is not

included.

Looking at the produced estimates of ESC about the limiting factors (Figure 3.12), for 23 out of 45 sample sites accumulated temperature appears to be the most important limiting variable. Soil moisture regime is limiting for only 5 sites, whereas continentality and soil nutrient regime for 3 sites respectively. Moisture deficit on the other hand, does not appear which suggests that ESC translated any differences in productivity as an effect of temperature and not as spring-summer drought. Nevertheless, the appearance of continentality showed that ESC was able to capture the north-south and east-west variability in production.

Despite the fact that a large percentage of the variation in Scots pine growth was explained by site conditions, a large proportion of variance remained unexplained. Previous studies supported that a difference in height development could be the result of genetic variation. Perks and McKay (1997) and Perks and Ennos (1999) showed that western provenances of Scots pine (Glen Affric) had poor height and diameter development than eastern provenances (Abernethy). This could also have been the case with our study stands, as native genetic material was included in our sample mainly on the west side of the country, whereas commercial stands on eastern coastal areas might have come from a different material.

Initial planting density could also have affected height development (MacFarlane *et al*., 2000), with a very high density strongly reducing the dominant tree height. A portion of the variation in productivity may also be explained by the application of different management practises. Although rotation lengths and pre-commercial thinnings followed standard procedures, different management may have been applied according to site conditions e.g., severe wind damage, recreational activities etc. Additionally, part of the variability included the presence of either first, second and third rotation stands.

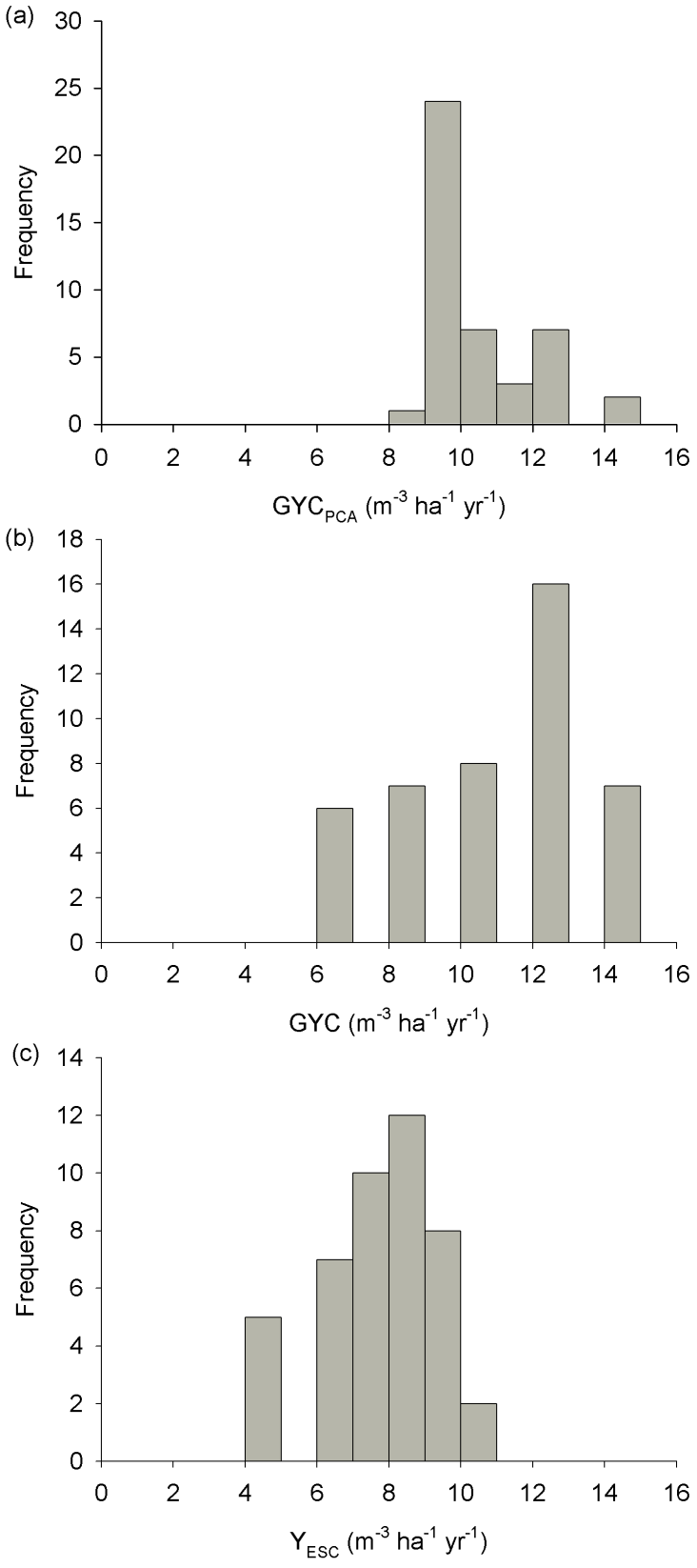

Figure 3.11: Histograms of yield class for (a) predicted values by the regression model (b) observed and (c) predicted by Ecological Site Classification

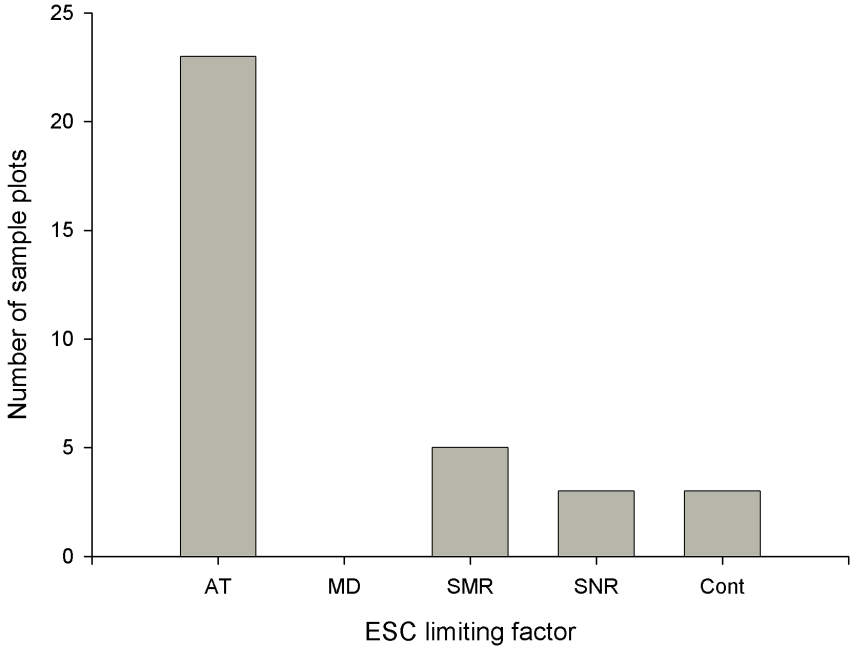

Figure 3.12: Limiting factors of Scots pine growth in Scotland as predicted by ESC

3.5 Conclusions

An extensive sampling scheme was undertaken to explore site conditions responsible for the differences in commercial stands of Scots pine in Scotland. Sites included in the study were as representative as possible of all growing conditions found across a range of elevations, latitude, longitude and soil type. Generally, the distribution of Scots pine production in Scotland could be described with a clear difference between east-west and north-south. The first signs of spring-summer drought was found to be the most significant for volume, biomass and height development for the east parts of the country something that verifies existing climate change scenarios. Scots pine also showed that it is a species capable to photosynthesis through out the year especially during those winter days were temperatures, sunshine and moisture are high enough to trigger photosynthetic activity. It also showed a preference for the most freely drained soils where nutrient concentration is not very high but with a preference in ammonium as the form of available nitrogen. Wind on the other hand, is a limiting factor for height development, whereas the elevational effect of the decline of productivity was

highlighted as with many other species. Nevertheless, additional sources of variability were present, perhaps due to genetic variations or different silvicultural treatments across stands.

We also employed the Ecological Site Classification to obtain a quick assessment of site characteristics such as soil texture and ground vegetation. ESC can provide a reliable information about the soil water and nutrient availability, however it shown that predictions of expected yield production were too conservative. ESC also supported the findings that temperature and solar radiation (through the continentality variable) is within the important factors for growth of Scots pine.

Multiple linear regression models on the other hand, were necessary to identify the major factors affecting growth. A more extensive soil survey including concentration of other important nutrient elements, soil physical characteristics and acidity, as well as competition indices, wind-related variables or genetic origin of the stands could provide additional useful information. However, the assumption of a linear relationship between dependent and independent variables and lack of a direct link to the physiological implications of site conditions, limits their application. Process-based models, coupled with a GIS system, may provide a way forward, by providing a better description of several ecosystem and physiological functions.

CHAPTER 4

Sensitivity and uncertainty analyses from a coupled 3-PG and soil organic matter decomposition model

4.1 Introduction

Process-based models describe the behaviour of a system through a set of functions based on physiological and biophysical processes occurring over time (Mäkelä, 2003). The complexity of the algorithmic representation is in most occasions very high. Process-based models simulate the production of a single tree or a stand using inputs such as mean temperature, rainfall and solar radiation. Photosynthesis, respiration, biomass allocation, nutrient utilisation and uptake, litterfall and root turnover are modelled based on physiological principles (McMurtrie *et al*., 1992, BIOMASS) or biochemical principles (Running and Gower, 1991, FOREST-BGC) at a very fine time scale (hours, days). The more complex the model is, the smaller the time step and the greater the modelling resolution at which it operates (i.e., the lower the simulation level, e.g. leaf, tree, stand, region or globe), which consequently increases the number of parameters required for parameterisation and initialisation. Models differ on the way the principal processes are represented. For example BIOMASS and MAESTRO (Wang and Jarvis, 1990a,b) include a detailed description of canopy architecture to represent photosynthesis, where 3-PG (Landsberg and Waring, 1997) assumes a one layer canopy. Even detailed models such as BIOMASS and MAESTRO, differ in the way photosynthesis is modelled. MAESTRO includes different canopy shapes whereas BIOMASS assumes three layers of canopy with equal shape. Obtaining a fairly simple model with

high generality, but with the same physiological principles, requires to decrease the modelling resolution and time step. Such models can be useful not only for research but for management too (Johnsen *et al*., 2001). The last few years there is an extensive effort to introduce simplified process-based models such as 3-PG for use not only as a research tool but also for forest management (Landsberg and Waring, 1997; Johnsen *et al*., 2001; Landsberg *et al*., 2003; Mäkelä, 2003).

4.1.1 Review

4.1.1.1 On 3-PG

The model appeared in the literature about ten years ago by Landsberg and Waring (1997) but the main principles of the model can been be traced from earlier work. Landsberg (1986) and Landsberg and Gower (1997) give a description of the quantum yield efficiency and of its use in the estimation of gross primary production. The use of allometric coefficients are also reported in Landsberg (1986).

Since its publication, 3-PG has been tested in many different parts of the globe. It has been frequently used as a research tool (Waring, 2000; Coops *et al*., 2001a,b; Landsberg *et al*., 2001; Whitehead *et al*., 2002) and the majority of the literature is focused on improving perceived weaknesses (Sands and Landsberg, 2002; Hirsch *et al*., 2003; Landsberg *et al*., 2003; Stape *et al*., 2004). 3-PG was integrated into GIS for spatial predictions of forest productivity (Tickle *et al*., 2001a,b) and even utilises remote sensing data as inputs for simulations (Coops *et al*., 1998, 2001a,b; Landsberg *et al*., 2003). It has been combined with other process-based models with the objective f reducing the potential errors derived from its assumptions (Liu *et al*., 2002; Peng *et al*., 2002; Paul and Polglase, 2004). It has been used as a tool to reduce the gap between ecosystem flux measurements and process-based ecosystem models (Law *et al*., 2001; Whitehead *et al*., 2002; Landsberg *et al*., 2003).

3-PG has been also used across several biomes. From Australian *Eucalyptus* plantations (Coops *et al*., 1998; Tickle *et al*., 2001a; Sands and Landsberg, 2002) and

Sitka spruce plantations in Great Britain (Waring, 2000) to lodgepole pine in USA and *Pinus patula* Schlecht. and Chamisso in South Africa (Dye, 2001), rimu in New Zealand (White *et al*., 2000; Whitehead *et al*., 2002), tropical species of the Amazon basin (Hirsch *et al*., 2003, 2004; Stape *et al*., 2004) and recently Scots pine in Finland (Landsberg *et al*., 2005).

Hirsch *et al*. (2003) used 3-PG to model the spatial pattern of forest productivity and potential biomass accumulation in the Amazon basin and observed that the limiting factor for forest growth during recovery from deforestation was the available soil water. The authors suggested that the outcome might have resulted from a model's weakness in modelling soil water or because of the lack of varying Fertility Rating during the simulation period. Additionally, they highlighted the need to model in more detail water and respiration processes but also fertility, land use and flammability. This conclusion comes into complete agreement with the evaluation of the model by Landsberg *et al*. (2003), who also detected the need to improve the modelling of site fertility and consequently the estimate the FR parameter. Landsberg *et al*. (2003) also suggested that a possible way to solve this problem would be to introducing a dynamic soil organic matter model. Landsberg *et al*. (2003, and personal communication) also suggested the use of soil surveys for empirical estimation of the FR, however this method has species and site limitation.

The simulations by Whitehead *et al*. (2002) showed that a constrain in the fertility of rimu sites in New Zealand had to be adjusted manually in order for the output stem increment to match observed values. Nevertheless, this work demonstrated the relationship between quantum yield efficiency and nutrient availability. Thus highlighting the limitations of photosynthesis by site fertility. The weakness of 3-PG's fertility rating was also reported by Landsberg *et al*. (2001) for a loblolly pine experiment. On the other hand, Waring (2000) focuses also on quantum yield efficiency except from the soil fertility in a trial of 3-PG in Sitka spruce plantations in UK. He reported that the limiting factor for growth was primarily solar radiation and secondarily the soil fertility. He also highlighted the need to include the modelling of canopy nitrogen content and of solar radiation. In addition, Dye (2001), in his evaluation of 3-PG in

Pinus patula Schlecht. and Chamisso stands, mentioned that above ground biomass was under-estimated and different quantum yield efficiency and root allocation fractions had to be employed for the prediction to match the observations. The author also had to reduce root allocation values to more realistic ones, and notices that the rate of self-thinning was poorly predicted.

Dye (2001) in his study demonstrated the application of 3-PG in a wide range of growth conditions for *Pinus patula* Schlecht. and Chamisso in South Africa. The study concluded that 3-PG was able to realistically simulate growth patterns and water use of plantations with different rotation. The model parameterisation based on field data using simple physiological techniques was also interesting. Biomass data, litterfall, leaf area and sap flow measurements was some of the measurements providing the data for calibration. Fertility rating was estimated assuming a relation with site index, which was calculated using a height - age relationship.

Two studies by Esprey *et al*. (2004) and Almeida *et al*. (2004) conducted a sensitivity analysis on the model. Esprey *et al*. (2004), provided a thorough investigation of model's parameters, their sensitivity and their non-linearity. The results showed high sensitivity for parameters related to biomass partitioning and allocation, fertility, quantum yield efficiency and the ratio of net to gross primary productivity (P_N:P_G). Additionally, maximum and optimum temperatures for growth gave highly non-linear functions with the latter having significant importance. Almeida *et al*. (2004) also performed a sensitivity analysis on a range of parameters investigating the effect on multiple outputs of the model, including diameter at breast height, foliage, stem and root biomass and stand volume. The results match those of Esprey *et al*. (2004), with the most sensitive parameters for growth being the quantum yield efficiency and the maximum canopy conductance. However, none of the above studies explored or quantified the uncertainty that comes with the use of parameters values extracted either from the literature or from field experience.

The attempt by Paul and Polglase (2004) and Peng *et al*. (2002) to combine 3-PG with other process-based models is also worth mentioning. Paul and Polglase (2004) used 3-PG (for forest growth) combined with CAMFor (a carbon account model), GEN-

DEC (a litter decomposition model) and Roth-C (a soil carbon turnover model). On the other hand, Peng *et al*. (2002) used the coupled version of 3-PG with TREENYD3 (Bossel, 1996) and CENTURY4.0 (Parton *et al*., 1993) developed by Liu *et al*. (2002). The study presented one approach of reusing ecosystem models in a hybrid way to overcome any disadvantage of the individual models. In TRIPLEX, 3-PG's lack of soil organic matter decomposition and nutrient release is overcome by the routines of CENTURY, while the problematic stem mortality is substituted by the TREENYD3. Although such combinations may provide the solution for a complete process-based ecosystem modelling, the increase in complexity and in the number of parameters dramatically decreases their use for decision-making. However, the general idea of this study should not be discarded.

The principal of "recycling" or reusing ecosystem models in an integrated approach was also demonstrated in a more recent study by Hirsch *et al*. (2004). They used 3-PG as the basic forest productivity model coupled with a customised version of Roth-C model to account for the carbon budget of the Brazilian Amazon basin and the changes under different land uses. Additionally, they conducted an uncertainty analysis using a Monte-Carlo approach and a sensitivity analysis. The results showed that the model was most sensitive to parameters related to carbon allocation to wood, such as the ratio between net and gross primary productivity, the allocation coefficients and the turnover rates. However, the soil carbon parameters had a little effect on the ecosystem carbon storage. Finally, they pointed out the large sensitivity of the model to maximum temperature. A possible explanation is the indirect effect of temperature on growth thought the non-linear relationship with vapour pressure deficit, which affects stomatal conductance.

Despite the extended testing of the model and the continue updates, model developers continue to concentrate on the failures of the model to represent any nutrient status and effects on growth. However, the other spectrum of 3-PG's developments include the assumptions of constant quantum yield efficiency and P_N:P_G ratio. The first attempt to produce an efficient and relative simplistic canopy photosynthesis sub-model was presented by Duursma *et al*. (2004). The model represented canopy using ten layers of

foliage, for which shaded and sunlit assimilation rates at leaf level were estimated and scaled up to stand level. Nitrogen concentrations varied vertically in the canopy and affected photosynthetic rates. Gross primary production then integrated using intercepted photosynthetic active radiation and the effects of vapour pressure deficit and air temperature. In addition, some modifications on tree allometry was included. Model's applications on coniferous species however, failed to reproduce successfully field observation.

The latest application of 3-PG by Landsberg *et al*. (2005) is for *Pinus sylvestris* L. in Finland. The performance of the model was tested using long-term mensuration data to calibrate parameters. New modifications were applied on the allocation routine of the model while the allocation parameters were calculated from field data. One interesting point discussed by the authors is the necessary alterations introduced on the allocation parameters of the model. The aim was to increase the values of modelled foliage biomass since foliage turnover was greater than stem turnover. The allocation problem was also discussed by Duursma *et al*. (2004) who suggested that the problem arose from the fact that mean diameter and mean stem biomass are not related by the same allometric relation during the simulation time. Corrections were applied by adding the bias of mean diameter estimation to satisfy the allometric relation. In addition, they proposed a new approach to include the seasonality in foliage mass by assuming that growth occurs during one month in spring. This way, leaf area index (L^*) was higher in the summer and lower in the winter. This supports the observations by Landsberg *et al*. (2005) that foliage allocation was lower when model simulated coniferous species. 3-PG has also been integrated with forest patch-models such as PICUS (Seidl *et al*., 2005) and GROWEST (Zuo *et al*., 2003). 3-PG also comes with an investigation of the fertility on forest carbon storage after an integration with the process model SECRETS (Sampson *et al*., 2006), the prediction of site index across Oregon in USA using 3-PG SPATIAL (Swenson *et al*., 2005) and the application of 3-PG for simulating tree growth in Australia in point and spatial mode (Bugg *et al*., 2006).

4.1.1.2 On ICBM

The model was introduced by Andrén and Kätterer (1997), as a simple soil carbon balance model for agricultural use. Kätterer and Andrén (1999) used ICBM to investigate the influence of management on soil carbon stocks for agricultural fields in Northern Europe. On the other hand, Andrén *et al*. (2001) used ICBM to investigate the influence of soil fauna on soil carbon balance. Finally, Kätterer and Andrén (2001) used the ICBM family in a series of experiments to evaluate their use.

The first and most simple version of the model, included two carbon pools as initial state variables, one ”young” for the freshly decomposed litter and one ”old” for the humified litter. It also included five parameters, i.e. constant decomposition rates (k_Y and k_O for young and old pool respectively), a humification coefficient representing the rate of which carbon enters the old pool, a parameter to represent the response of decomposition (r_e) to external variables and the input (i), which includes litterfall and root turnover. Kätterer and Andrén (2001) presented five other versions of the model including ICBM/2, a model with three carbon pools, ICBM/2B with two carbon and one microbial biomass pool, ICBM/N with two carbon and two nitrogen pools, ICBM/2N with three carbon and nitrogen pools and ICBM/2BN with three carbon, three nitrogen and one microbial biomass pool. The advantage of the ICBM family of models comes with the choice of using either the differential or analytically solved format.

Despite the different biomes in which 3-PG and ICBM have found their initial application, the two models have already been used alongside to study the carbon cycle of forest ecosystems (Borghetti and Magnani, 2003; Magnani *et al*., 2005). 3-PG was integrated with the simpler version of ICBM as a suitable stand ecosystem carbon dynamics simulator. The model was fitted to observed chronosequence data from a variety of biomes, including *Pinus sylvestris* L. from Finland and Sweden, *Picea sitchensis* (Bong.) Carr. from UK, *Pinus pinaster* Aiton from France and *Quercus cerris* L. from Italy. The models (described as 3PG-3) were used as a tool to extrapolate the observation data across time and to compare carbon fluxes across biomes. The two models

were integrated in such a way that 3-PG supplied the litter input for the ICBM routines. However, the project failed to include the effects of soil organic matter decomposition in ICBM on nutrient release and potentially on plant growth of 3-PG.

4.1.1.3 Our approach

Responding to the well documented limitation of 3-PG to include the effect of decomposition and nutrient release on plant growth, and wanting to develop a full ecosystem model with the simple physiological principles of 3-PG, we developed an integration strategy between the two models. We coupled them with a closed loop, with the output of one providing the input for the other. First, we describe the structure of the two models. We present the integration procedure and the basic principles behind it. Then, we present the calibration strategy followed to identify most of the species depended parameters for Scots pine (*Pinus sylvestris* L.) in Scotland. We provide a description of our calibration strategy based on a Bayesian approach using field data. Finally, we quantify the uncertainty of the parameters based on the results of the Bayesian calibration and we present the model performance and results of a sensitivity analysis of some of the basic outputs.

4.1.1.4 Definitions

Before the description of the model a brief array of some important definitions of the terminology used is necessary for a better understanding of both the model and the results. As mentioned in Chapter 1, mathematical models consist our effort to provide a quantitative understanding of plant mechanisms (Thornley and Johnson, 1990).

Input of a model is considered the process of providing and transferring information or data from the user to the mathematical model for either initialisation or per time step calculations and they could either be constants or time series. Time step is defined as the temporal scale for which each model calculation is iterated. Every model has variables and parameters. Variable is a quantity that can have any set of values and which can vary with time or in relation to any other variable. Parameter on the other

hand, is defined as a constant quantity which represents the rate of change between to changing quantities (i.e., variables). Parameters although they are constants, their values are often affected by other variables.

Finally, some definitions are necessary of the analysis performed. Sensitivity analysis of a model is considered the process for which a certain parameter is changed over a certain percentage and the equivalent change pattern of a set of output variables is observed. The process is able to identify extreme model feedback, that is model outputs which are likely to have an extreme response when a small or a large change of a certain parameter occurs. On the other hand, uncertainty analysis is the process of quantifying the uncertainty in model predictions. Thus, uncertainty is defined as the quantity representing the error related to the prediction of a model output.

4.1.2 Model description

4.1.2.1 The 3-PG

3-PG follows the conventional structure of a process-based model, that is, photosynthesis and respiration, allocation and senescence, environmental and soil effects on growth. However, it cannot be considered a complete ecosystem model because it lacks basic soil organic matter decomposition and respiration losses. The main inputs of 3-PG are climatic and site information. A list of all equation's initial state variable can be found in Table 4.1 and a list of parameters and their values can be found in Table 4.2, while a more detailed description of the model is given by Landsberg and Waring (1997) and Sands and Landsberg (2002).

Weather inputs could be actual monthly values or monthly averages over a period of years for mean monthly maximum and minimum temperature, rainfall and solar radiation. Vapour pressure deficit (VPD) is also a required input that can be derived from maximum and minimum values of temperature whereas frost and rain days are optional inputs. In addition, 3-PG requires an indication of nutritional status, which is provided through the Fertility Rating parameter (FR), having values between 0 and 1,

Table 4.1: Initial biomass state variables, soil status and meteorological inputs of the 3-PGN model.

Initial parameter	Variable	Units
Initial state variables		
Initial foliage biomass	W_{F_i}	$\mathrm{tDM\,ha^{-1}}$
Initial stem biomass	W_{S_i}	$\mathrm{tDM\,ha^{-1}}$
Initial root biomass	W_{R_i}	$\mathrm{tDM\,ha^{-1}}$
Initial young labile carbon pool	$Y_{l\ i}$	$\mathrm{tC\,ha^{-1}}$
Initial young refractory carbon pool	Y_{r_i}	$\mathrm{tC\,ha^{-1}}$
Initial old carbon pool	O_i	$\mathrm{tC\,ha^{-1}}$
Initial young labile nitrogen pool	Y_{Nli}	$\mathrm{tN\,ha^{-1}}$
Initial young refractory nitrogen pool	$Y_{N_{ri}}$	$\mathrm{tN\,ha^{-1}}$
Initial old nitrogen pool	O_{Ni}	$\mathrm{tN\,ha^{-1}}$
Soil status		
Maximum available soil water capacity	$MaxASW$	mm
Minimum available soil water capacity	$MinASW$	mm
Soil class (S, SL, CL, C)	$SoilClass$	-
Meteorological inputs		
Monthly mean daily maximum temperature	Tmax	°C
Monthly mean daily minimum temperature	Tmin	°C
Monthly mean temperature	Tav	°C
Monthly rainfall	-	$\mathrm{mm\,month^{-1}}$
Monthly mean daily pan evaporation	-	$\mathrm{mm\,day^{-1}}$
Monthly mean daily solar radiation	-	$\mathrm{MJ\,m^{-2}\,day^{-1}}$
Rainy days per month	-	$\mathrm{day\,month^{-1}}$
Frost days per month	-	$\mathrm{day\,month^{-1}}$
Monthly mean vapour pressure deficit	VPD	mBar

with zero indicating an infertile site. Most of the existing process-based models, simulate processes within an individual tree using a daily time step. In that respect 3-PG is simplified, as it simulates productivity at the stand level using a monthly time step.

$$P_G = \alpha_c \phi_{pa} = \alpha_x f_T f_N f_F \varphi \phi_{pa} \tag{4.1}$$

Table 4.2: Description of 3-PGN parameters and values for Scots pine. Calibration procedure included the exploration of the posterior distribution of 32 dimension parameter space using Bayes' theorem and Monte Carlo Markov Chain simulation. Parameters which were not included in the procedure were chosen from literature.

Parameter description	3-PGN symbol	Units	*Pinus sylvestris* L.
Allometric relationships partitioning			
Foliage:stem partitioning ratio at D=2 cm	p_{FS_2}	-	0.76
Foliage:stem partitioning ratio at D=20 cm	$p_{FS_{20}}$	-	0.46
Constant in the stem mass v. diam. relationship	a_s	-	0.0572
Power in the stem mass v. diam. relationship	n_s	-	2.4568
Maximum fraction of NPP to roots	n_{Rx}	-	0.48
Minimum fraction of NPP to roots	n_{Rn}	-	0.21
Temperature modifier			
Minimum temperature for growth	T_{min}	°C	-5
Optimum temperature for growth	T_{max}	°C	15
Maximum temperature for growth	T_{max}	°C	35
Frost modifier			
Days production lost per frost day	kF	days	1
Soil water modifier			
Moisture ratio deficit for fq = 0.5	SW_{const}	-	site specific
Power of moisture ratio deficit	SW_{power}	-	site specific
Fertility effects			
Value of "m" when FR = 0	m_0	-	0
Value of "f_N " when FR = 0	f_{N_0}	-	0.6
Age modifier			
Maximum stand age used in age modifier	F_a	years	120
Power of relative age in function for fAge	n_{age}	-	4
Relative age to give fAge = 0.5	$rAge$	-	0.75
Litterfall and root turnover			
Maximum litterfall rate	γ_{F_x}	month^{-1}	0.024
Litterfall rate at t = 0	γ_{F_0}	month^{-1}	0.0022
Age at which litterfall rate has median value	t_{γ_F}	month	60
Average monthly root turnover rate	$Rttover$	month^{-1}	0.07
Conductance			
Maximum canopy conductance	g_{c_x}	$\mathrm{m\ sec}^{-1}$	0.02
Leaf area index for maximum canopy conductance	$L^*_{g_{c_x}}$	-	3.33
Defines stomatal response to VPD	$CoefCond$	mBar^{-1}	0.05
Canopy boundary layer conductance	g_{BL}	$\mathrm{m\ sec}^{-1}$	0.2
Stem numbers			
Max. stem mass per tree at 1000 trees/hectare	$w_{Sx_{1000}}$	$\mathrm{kg\ tree}^{-1}$	255
Power in self-thinning rule	n_m	-	1.5
Fraction mean single-tree foliage biomass lost per dead tree	mF	-	0.2
Fraction mean single-tree root biomass lost per dead tree	mR	-	0.2
Fraction mean single-tree stem biomass lost per dead tree	mS	-	0.2
Canopy structure and processes			
Specific leaf area at age 0	σ_0	$\mathrm{m}^2\ \mathrm{kg}^{-1}$	6
Specific leaf area for mature leaves	σ_1	$\mathrm{m}^2\ \mathrm{kg}^{-1}$	4
Age at which specific leaf area $= (\sigma_0 + \sigma_1)/2$	t_σ	years	6
Extinction coefficient for absorption of PAR by canopy	k	-	0.52
Age at canopy cover	$fullCanAge$	years	18
Maximum proportion of rainfall evaporated from canopy	I_x	-	0.15
LAI for maximum rainfall interception	$L^*_{I_x}$	-	5
Canopy quantum efficiency	α_x	$\mathrm{molC\ molPAR}^{-1}$	0.05
Branch and bark fraction			
Branch and bark fraction at age 0	p_{BB_0}	-	0.3
Branch and bark fraction for mature stands	p_{BB_1}	-	0.1
Age at which branch and bark fraction $= (\mathrm{p_{BB_0}} + \mathrm{p_{BB_1}})/2$	t_{BB}	years	10
Various			
Ratio NPP/GPP	Y	-	0.49

Table 4.2: *Continued*

Parameter description	3-PGN symbol	Units	*Pinus sylvestris* L.
Basic density	ρ	$\mathrm{t\ m^{-3}}$	0.39
Conversion factors			
Intercept of net v. solar radiation relationship	Qa	$\mathrm{W\ m^{-2}}$	-90
Slope of net v. solar radiation relationship	Qb	-	0.8
Molecular weight of dry matter	gDM_mol	$\mathrm{gDM\ mol^{-1}}$	24
Conversion of solar radiation to PAR	$molPAR\_MJ$	$\mathrm{mol\ MJ^{-1}}$	2.3
ICBM/2N			
Decomposition rate constant for the young and labile pool	$k_{l_{max}}$	$\mathrm{month^{-1}}$	0.0315
Decomposition rate constant for the young and refractory pool	$k_{r_{max}}$	$\mathrm{month^{-1}}$	0.0042
Decomposition rate constant for the old pool	$k_{o_{max}}$	$\mathrm{month^{-1}}$	0.0005
Humification coefficient	h_c	-	0.2308
Quality, C:N ratio of refractory litter input	q_{i_r}	-	334.29
Quality, C:N ratio of labile litter input	q_{i_l}	-	49.08
C:N ratio of humification	q_{h_c}	-	23.63
C:N ratio of soil organism biomass	q_{b_c}	-	2.21
Efficiency of labile pool	e_l	-	0.25
Efficiency of refractory pool	e_r	-	0.56
Foliage nitrogen concentration	N_{c_f}	-	1.48

Intercepted photosynthetic active radiation (ϕ_{pa}) is calculated from incoming solar radiation. Gross primary production (P_G) is a product of ϕ_{pa} and quantum yield efficiency (α_c, see also Equation 4.1). Environmental limitation on growth is accounted through a series of modifiers including air temperature (f_T), frost (f_F), nutritional status (f_N) while physiological effect (φ) is accounted through modifiers for age (f_{AGE}), soil water (f_θ) and vapour pressure deficit (f_{VPD}), with all modifiers having values from 0 to 1. The modifiers constrain the maximum quantum yield efficiency (α_x) to its effective value α_c.

$$\varphi = f_{AGE} \min\{f_{VPD} f_\theta\} \tag{4.2}$$

Net primary production (P_N) is derived using a constant ratio (0.45±0.05 Landsberg and Waring, 1997; Waring *et al.*, 1998) to account for respiration losses. This is an assumption that reduces the complexity of the model; nevertheless, it causes controversy in the scientific community (Mäkelä and Valentine, 2001). P_N is then allocated to three structural compartments, stem, roots and foliage, through a series of allocation coefficients estimated from empirical relationships (Landsberg, 1986; Landsberg

and Waring, 1997). All carbohydrates are allocated on a single-tree bases. Allocation occurs firstly to the root compartment (n_R), which is directly affected by site fertility (m) and water availability. Stem allocation is then estimated from a foliage:stem ratio using an allometric relation with diameter at breast height ($p_{FS} = a_p D^{n_p}$) whereas the remaining carbohydrate are allocated to foliage.

$$n_R = \frac{n_{Rx} n_{Rn}}{n_{Rn} + (n_{Rx} - n_{Rn}) m\varphi} \tag{4.3}$$

$$n_S = \frac{1 - n_R}{1 + p_{FS}} \tag{4.4}$$

$$n_F = 1 - n_R - n_S \tag{4.5}$$

Soil water balance is derived as a reduction of the incoming precipitation, by canopy interception and transpiration losses calculated using the Penman - Monteith formula (Landsberg and Waring, 1997). The model assumes loss of water by run-off when current soil water holding capacity exceeds a certain maximum value but with no explicit calculation. Leaf area index (L^*) is the product of an age-dependent specific leaf area (σ) and the current foliage biomass. Litterfall reduces foliage biomass monthly, based on a time depended litterfall rate (Sands and Landsberg, 2002). Natural mortality is accounted for using the self-thinning law, which is applied when the mean single tree above ground biomass exceeds a maximum value $w_{Sx_{1000}}$.

Stand volume (V) is estimated from stem biomass and basic wood density (ρ) multiplied by a branch and bark fraction. Current (CAI) and mean annual increments (MAI) are then derived as an function of age.

$$V = (1 - p_{BB}) W_S / \rho \tag{4.6}$$

$$p_{BB} = p_{BB_1} + (p_{BB_0} - p_{BB_1})\mathrm{e}^{-(\ln 2)(t/t_{BB})} \tag{4.7}$$

Standard model outputs include a wide range of variables interesting to both forest managers and forest ecologists, including annual and monthly values of stem (W_S), foliage (W_F) and root biomass (W_R), V, diameter at breast height (D) and basal area (G), MAI, total litterfall, P_N and P_G. Also, parameters such as total evapotranspiration, leaf area index, specific leaf area, growth modifiers and allocation coefficients complete the output set.

4.1.2.2 ICBM/2N

Different tree components (e.g., root and leaf woody debris) have different decomposition rates (Berg and Ekbohm, 1993; Titus and Malcolm, 1999; Hyvönen *et al.*, 2000; Mäkelä and Vanninen, 2000; Janssens *et al.*, 2002; Laiho and Prescott, 2004) and so the first version of ICBM was found inadequate for use. We chose ICBM/2N as the most appropriate to introduce different decomposition rates for different components without losing any of the required simplicity.

The model has two young pools for carbon, one "labile" (Y_l), which includes the fine woody debris (litterfall and fine root turnover) and a "refractory" pool (Y_r), which includes coarse woody debris (coarse roots and branches) with a lower decomposition rate. There is also an old pool (O), which represents the humified organic matter. Each pool has a constant decomposition rate (k_{Y_l}, k_{Y_r} and k_O for young and labile, young and refractory and old pool respectively) with a fixed external response (r_e). Usually, r_e is considered a constant but Kätterer and Andrén (2001) proposed an external response in relation to soil temperature and soil water potential. Finally, the humification coefficient (h_c), which applies to humification processes of both young pools, represents the rate at which carbon turns into humus. The model runs in annual time steps and the input is in units of carbon. The differential Equations 4.8, 4.9 and 4.10 indicate the changes of the state variables in each time step. Each carbon pool has a respiratory

loss due to decomposition, which is also affected by external (mainly environmental) conditions.

$$\frac{d}{dt}Y_l = i - k_{Y_l} r_e Y_l \tag{4.8}$$

$$\frac{d}{dt}Y_r = i - k_{Y_r} r_e Y_r \tag{4.9}$$

$$\frac{d}{dt}O = r_e h_c (k_{Y_l} Y_l + k_{Y_r} Y_r) - k_O r_e O \tag{4.10}$$

The same representation of initial state variables exists for nitrogen stocks. ICBM/2N simulates nitrogen based on the fluxes and stocks of carbon and through C:N ratios. In addition, two more parameters e_l and e_r represent the microbial efficiency for labile and refractory pool, respectively i.e., the fraction of C flux from the pool allocated to microbial growth. For more details about the structure and theory of the model see Andrén and Kätterer (1997) and Kätterer and Andrén (2001).

$$\frac{d}{dt}Y_{N_l} = \frac{i}{q_{i_l}} + k_{Y_l} r_e \left(\frac{e_l(1-h_c)}{q_{b_c}(1-e_l)} - \frac{h_c}{q_{h_c}}\right) Y_l - k_{Y_l} r_e \frac{1-h_c}{1-e_l} Y_{N_l} \tag{4.11}$$

$$\frac{d}{dt}Y_{N_r} = \frac{i}{q_{i_r}} + k_{Y_r} r_e \left(\frac{e_r(1-h_c)}{q_{b_c}(1-e_r)} - \frac{h_c}{q_{h_c}}\right) Y_r - k_{Y_r} r_e \frac{1-h_c}{1-e_r} Y_{N_r} \tag{4.12}$$

$$\frac{d}{dt}O_N = \frac{r_e h_c}{q_{h_c}} (k_{Y_l} Y_{lr} + k_{Y_r} Y_r) - k_O r_e O_N \tag{4.13}$$

Equations 4.11, 4.12 and 4.13 describe the changes of nitrogen stocks for the three state variables. Each young pool has inputs from above and below ground litter, which

is divided by the equivalent C:N ratio. Both young nitrogen stocks have a ”release” of nitrogen depending linearly on the decomposition rate and on external influence. Also, an input of nitrogen is added to each young pool by the microbial activity during the humification process. The final model, including both carbon and nitrogen compartment has six initial state variable and thirteen parameters which are listed in Table 4.2.

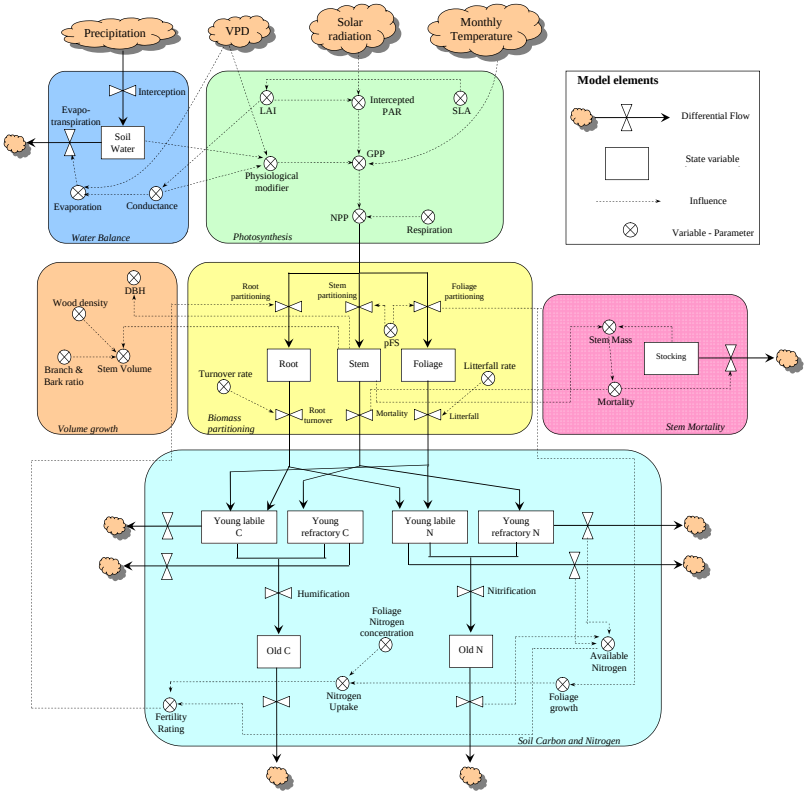

Figure 4.1: Flow diagram for the 3-PGN model. Boxes represent pools, circles represent variables or inputs and thick arrows represent fluxes in and out of the pools. Thine dashed arrows represent influences between variables and pools. There are six sub-models including water balance, photosynthesis, biomass partitioning, volume growth, stem mortality and soil carbon and nitrogen.

4.1.2.3 The 3-PGN model

The new model incorporates all the main features of 3-PG and ICBM/2N with a two-way dynamic integration, in such a way that SOM and nutrient dynamics could affect potential growth (Figure 4.1). However, since the nitrogen cycle has not represented explicitly in 3-PG such a modelling exercise required altering some of the basic principles, driving it to a complexity beyond the initial scope of the model. The way forward

was to introduce a new method of estimating the current, commonly accepted, weakly supported fertility rating. Our scope was not to change the way in which nutrient effects were represented within the model but to remove the need for manual manipulation of the fertility indicator and introduce a simple but process-based way to estimate it.

The first integration step included the supply of litter to carbon and nitrogen pools. Monthly litterfall of roots, foliage and stem were separated into labile and refractory carbon pools, with the first including foliage litter and root turnover, and the second including only stem mortality. Each pool was updated in a monthly time step and the differential equations in ICBM/2N were adjusted to run using the new time step. The driving factor for altering the time step of ICBM/2N was the ability to estimate and monitor the nutritional status of the stand at the same temporal scale as the outputs of the model.

The second integration step included the estimation of the nutritional status and its effect on productivity. The new way of deriving the Fertility Rating (FR) of 3-PG was based on estimating the ratio of "plant available" nitrogen (N_{AV}) to "nitrogen uptake" (U_N). Although nutrients such as phosphorus (P) and potassium (K) are considered to have significant effects on growth (Oleksyn *et al*., 2003; Ladanai and Ågren, 2004; Vestgarden *et al*., 2004) in order to keep the levels of complexity low we assumed nitrogen to be the most limiting nutrient for growth (Equation 4.14).

$$FR = \frac{N_{av}}{U_n} \tag{4.14}$$

By "plant available" nitrogen we considered the mineral form of nitrogen available for the plant roots to take up dissolved in the soil solution. This quantity is estimated by ICBM/2N (Equation 4.15). The three nitrogen pools of the model have three outfluxes dependent on decomposition rates representing either loss of nitrogen from leaching or uptake by plants. We assumed that no nitrogen is lost through leaching and that all three quantities added give the plant available nitrogen.

$$
\begin{aligned}
N_{av} &= k_{Y_l}(\frac{1-h_c}{1-e_l})Y_{N_l} - e_l\frac{Y_l}{q_{b_c}} \\
&+ k_{Y_r}(\frac{1-h_c}{1-e_r})Y_{N_r} - e_r\frac{Y_r}{q_{b_c}} + k_O O_N
\end{aligned} \tag{4.15}
$$

The uptake rate of nitrogen is estimated based on a theory described by Landsberg (1986), in which the uptake rate of a nutrient by the plant is proportionally related to its concentration in each structural tissue and the growth rate of the respective tissue (Equation 4.16).

$$
U_i = \sum_{i=F,S,R} [M_i]\frac{dW_i}{dt} \tag{4.16}
$$

Due to the fact that nitrogen becomes more important in the foliage where photosynthesis is taking place we ignored nitrogen concentrations of stem and roots. Additionally, recent studies (Mencuccini and Grace, 1996; Korakaki, 2003) show that foliage nitrogen concentrations of Scots pine needles do not change significantly with age and so it is assumed constant. Thus, for the stand to keep foliage nitrogen concentration constant, nitrogen is extracted from the soil and foliage biomass increases.

Following the estimation of nitrogen uptake rate and availability of nitrogen the ratio of FR is estimated. It must be noticed that the ratio still takes values between 0 and 1, with one indicating that the availability of nitrogen exceeds the uptake rate and so the site could be considered fertile. In such a scenario, 3-PG will allocate less to roots and more to foliage and stem, which will increase the foliage growth rate. This will be followed by an increase in nitrogen uptake and a decrease in FR. Additionally, we must bring to attention that the above ratio does not explicitly remove any nitrogen quantities from the soil. The new way of estimating FR only provides an indication of the potential fertility and is re-estimated in each time step according to the current soil and stand growth conditions. FR continues to affect the root allocation coefficient and

the nutritional environmental modifiers affecting quantum yield efficiency. 3-PGN (3-PG Nitrogen) removes the need for any manual manipulation of FR to match empirical knowledge or estimations from soil survey data of site fertility, although this is still an option within the model. The initialisation of the FR is through the initialisation of ICBM state variables of carbon and nitrogen pools.

To include directly the effects of climate on the decomposition of SOM and to nutrient release we also need to modify the equations of ICBM/2N. More specifically, we removed the user-defined parameter r_e and we made decomposition a linear function of air temperature and soil moisture through the environmental modifiers of 3-PG. The maximum values of decomposition rates for labile young, refractory young and old carbon pools ($k_{l_{max}}$, $k_{r_{max}}$ and $k_{o_{max}}$ respectively) are reduced by the estimated f_T and f_θ of 3-PG (see eqs.4.17, 4.18 and 4.19). The modelling comes in agreement with other well-established process-based models (Running and Gower, 1991; Aber *et al.*, 1992; Parton *et al.*, 1993). However an assumption that air temperature affects the decomposition instead of soil temperature is made.

$$k_{Y_l} = k_{l_{max}}\, f_T\, f_\theta \tag{4.17}$$

$$k_{Y_r} = k_{r_{max}}\, f_T\, f_\theta \tag{4.18}$$

$$k_O = k_{o_{max}}\, f_T\, f_\theta \tag{4.19}$$

It is possible that the temperature modifier of tree growth used here introduces a bias in the estimation of the soil decomposition rates since the optimum temperature for growth is not necessarily identical to the optimum temperature for decomposition. The way to avoid such a bias would be to introduce a soil temperature modifier by using average, maximum, minimum and optimum temperatures for decomposition. However

such an introduction would need soil temperature inputs, which in most occasions are difficult to find.

4.2 Materials and methods

4.2.1 Data source

4.2.1.1 Stand level data

Scots pine (*Pinus sylvestris* L.) is a species found across different environments in Scotland, from the humid and windy west to the less humid and more continental climate of the east. It covers and area of 219,438 hectares of pure monoculture stands, 73,421 hectares of which are under Forestry Commission ownership (Forestry Commission, National Inventory of Wooldlands and Trees, 2003). Almost half of the total area of Scots pine is native woodlands (135,313 ha, Mason *et al*., 2004). To explore the differences in productivity and to produce a parameter set which captures those differences, we considered several sites across the country.

Table 4.3: Information about the location and topography for the six plots used in the uncertainty analysis and obtained from Forestry Commission Permanent Sample Plots and the eight calibration plots obtained from an extensive field survey across Scotland conducted during this project.

	Longitude (°W)	Latitude (°N)	Aspect (degrees)	Slope (degrees)	Elevation (m)
FC Permanent Sample Plots					
Site 1	3°29.0′	57°40.7′	27	1	3
Site 2	3°27.7′	57°41.3′	186	1	13
Site 3	3°41.5′	57°37.6′	0	0	8
Site 4	4°16.9′	57°36.4′	312	4	173
Site 5	4°19.2′	57°35.9′	310	2	112
Site 6	3°04.0′	57°37.3′	135	2	70
Field Survey Plots					
Plot 1	3°06.3′	55°37.2′	34	15	324
Plot 5	4°30.8′	55°05.1′	138	4	79
Plot 9	4°01.5′	56°35.5′	350	16	342
Plot 10	3°16.4′	57°20.7′	156	15	367
Plot 14	3°27.4′	55°52.0′	324	1	212
Plot 22	3°11.2′	57°41.4′	0	0	5
Plot 30	3°51.3′	57°08.0′	207	2	305
Plot 46	4°16.1′	58°27.7′	272	4	122

The data for calibration and validation of 3-PGN came from the permanent sample plot (PSP) data base of UK Forestry Commission. The 51 experimental plots of Scots pine received different silvicultural treatments as a part of thinning experiment. The data base included control plots, stands with low, "neutral" and crown thinning and provided information about mean diameter, top height, basal area, stocking and standing volume as a time series for each plot for some plots up to 125 years. Stem, foliage and root biomasses were calculated for each stand using pooled allometric equations developed for Scots pine (Ovington, 1957; Albrektson, 1980; Vanninen *et al*., 1996; Oleksyn *et al*., 1999; Xiao *et al*., 2003) (see Chapter 3). Field visit to 23 of the plots provide information about soil texture and water content. Table 4.3 shows the six sites used for calibration and uncertainty analysis. Eight validation plots came from the same dataset. Control plots were used for both calibration and validation purposes, as no information was available on the intensity of thinning applied in them, in order to device a thinning regime for 3-PGN.

Additionally to the PSP data set, an extensive field survey of 45 plots was established across the country, sampling pure commercial stands of Scots pine with different climatic and elevational conditions. The measurements included height, productivity and soil information like soil texture, water content and carbon and nitrogen stocks. Eight plots were extracted from this data set, to represent a range of elevations and latitudes and were included in the calibration analysis (Table 4.3).

4.2.1.2 Climate

Although the calibration procedure of the model is for particular sites and despite the fact that a well established network of meteorological stations exist across the UK, we wanted to provide climate inputs for the model at any geographical location and at the same time create a spatially interpolated data set. To create such surfaces, we used a dataset obtained from the Climate Research Unit of the University of East Anglia (CRU). The dataset is a 10km point-grid including mean monthly averages of maximum and minimum temperature, precipitation, rain days, frost days, sunshine hours and relative humidity for the period 1961 - 1997 across Great Britain. For each data

point the values are provided for a low, a high and an average elevation. To account for any bias introduced in the prediction due to variation with elevation we used the values at average elevation.

Before we proceeded with any interpolation we investigate thoroughly the spatial variation of each variable. Our target was to provide the best possible quality of spatial data set as climatic inputs are key driving factors for 3-PGN. We applied several geostatistical and deterministic interpolation techniques to identify the methodology providing the small bias and the better fit between observed and predicted values. Before that the spatial variation was explored by creating variograms of each variable and exploring for any spatial trends. Then we applied ordinary, simple and universal kriging, ordinary and simple co-kriging, splines with tension, thin plate splines and inverse distance weight. From each method the root mean squared error was compared as an indication of fitness of predicted to observed values. Mean prediction error provide information about the bias of the estimation, where average prediction error gave an indication of overestimation or underestimation. Based on the above, we identified the interpolation method which provided the smallest bias and best fit between observed and predicted values. A digital elevation model in a 50m resolution provided by Ordnance Survey UK was also used as a second variable for co-kriging.

Additionally to temperature and precipitation surfaces, we created surfaces of latitude, frost days and relative humidity. The first two variables were used as input for the 3-PG model, whereas the latter ones were used to estimate incoming solar radiation based on monthly averages of temperature and precipitation (see below). Results were masked for Scotland with a 1km resolution.

4.2.1.3 Solar Radiation

Incoming solar radiation is a key driving factor for almost all eco-physiological models including 3-PGN. Such data often are not widely available from meteorological stations so several techniques have been developed over timer for their estimation. The more empirically based techniques included relationships of incoming solar radiation

with daily maximum and minimum temperature using transmitivity (Bristow and Campbell, 1984; Coops *et al*., 2000), or relationships between solar radiation and sunshine hours (Rietveld, 1978; Goodale *et al*., 1998).

The most popular technique based on transmitivity (presented by Bristow and Campbell, 1984) is widely used (Coops *et al*., 2000; Waring, 2000) although many improved versions also apply corrections for topography (Kumar *et al*., 1997; McKenney *et al*., 1999; Kang *et al*., 2002), clear-sky transmittance (Thornton and Running, 1999; Thornton *et al*., 2000) or for estimating diffuse and direct radiation on horizontal and inclined slopes (Kang *et al*., 2002). The technique has also been applied using spatial surfaces either of climatic inputs or digital elevation models (DEM) as driving factors (Kumar *et al*., 1997; Goodale *et al*., 1998; McKenney *et al*., 1999; Kang *et al*., 2002).

A more physically sound approach uses inputs of sun angle, latitude, slope and aspects for estimating diffuse and direct radiation (Swift, 1976; Brock, 1981; Nikolov and Zeller, 1992), as well as inputs of air temperature, precipitation and relative humidity to apply corrections for the estimated radiation proportions. Other studies used geostatistics to spatially interpolate data from weather station, when a good network exists (Rehman and Ghori, 2000), while more recent work applied artificial neural networks to provide regional estimates of solar radiation (Mohandes *et al*., 1998; Antonic *et al*., 2001; Dorvlo *et al*., 2002). The temporal scale is usually a day (Brock, 1981), but often algorithms use monthly inputs (Nikolov and Zeller, 1992). In any case, the use of a Geographic Information System (GIS) and the DEM is increasingly important.

We estimated incoming solar radiation using the algorithm by Nikolov and Zeller (1992), which is a general algorithm using inputs of monthly average temperature, total precipitation, relative humidity and applies corrections for topography by using latitude, elevation, slope and aspects. The algorithm has been tested for the whole northern hemisphere, at a range of sites from subpolar regions to the tropics, and it showed quite accurate seasonal patterns. We ran the algorithm within the ArcInfo workstation environment using our existing spatial dataset of monthly climatic inputs and topographic variables extracted from a DEM provided by Ordnance Survey of UK.

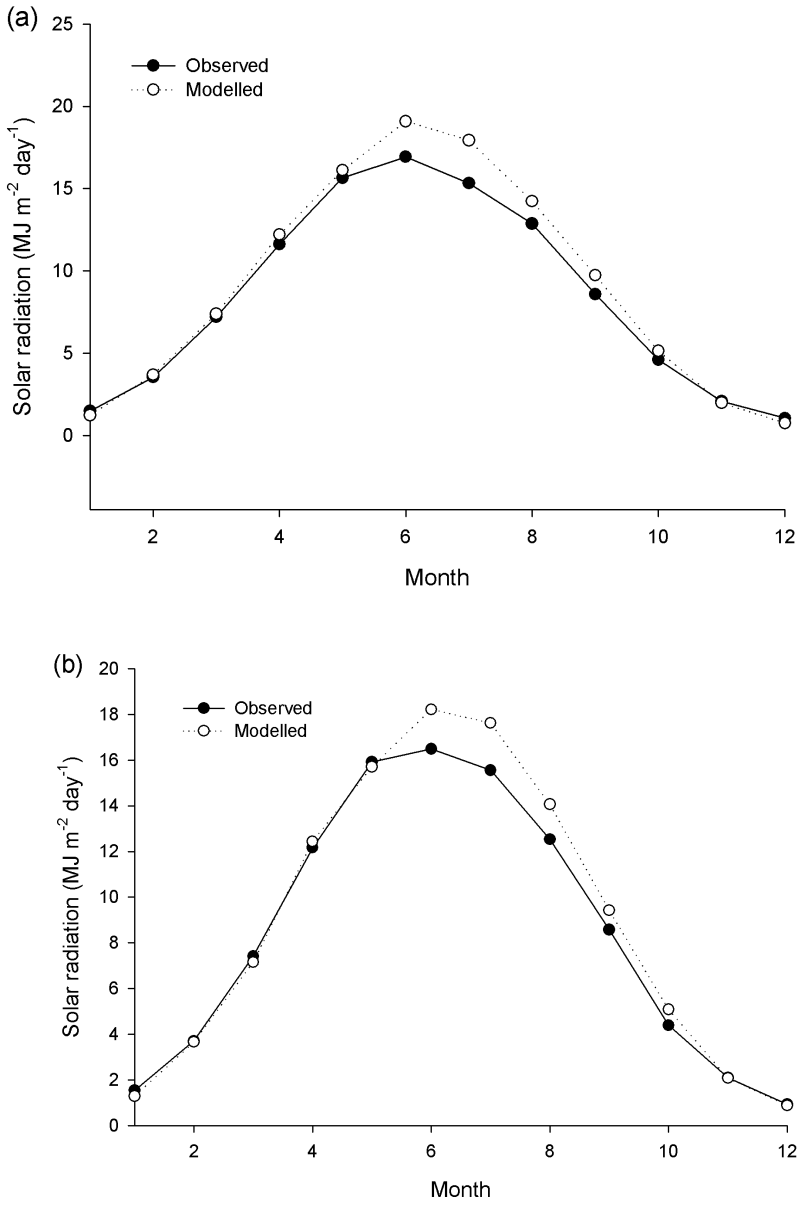

Figure 4.2: Modelled (empty circles) and observed (filled circles) patterns of solar radiation ($\mathrm{MJ\ m^{-2}\ day^{-1}}$) for the two validations sites: (a) Aberdeen (Longitude: $2°8.4'$ W, Latitude: $57°7.7'$ N, UK MetOffice weather station, data from `http://badc.nerc.ac.uk/home/`) (b) Griffin forest, EUROFLUX project experimental site (Longitude: $3°48'$ E, Latitude: $56°73'$ N, data from `http://www.fluxnet.ornl.gov/fluxnet/`).

The algorithm first estimates the incoming solar radiation at the top of the atmosphere based on the Julian day (J), solar declination (D_s), solar sunrise/sunset hours (h_s) and latitude (Lat). Radiation at the earth's surface is estimated by reducing radiation on the top of the atmosphere by an amount corresponding to the extent of cloudy atmospheric conditions (C, Equation 4.20). Cloudiness is calculated using mean monthly

water vapour pressure (e_v) and total precipitation (P) (Equation 4.20), whereas mean monthly water vapour pressure is estimated using an exponential relationship with relative humidity and mean monthly temperature (Equation 4.21).

$$C = 10 - 1.155(e_v/P)^{0.5} \tag{4.20}$$

$$e_v = H_r 6.1078 \exp[17.269T/(T + 237.3)] \tag{4.21}$$

The empirical coefficients of Equation 4.21 are derived through a relation with Lat using data from a range of latitudes including sites from the whole northern hemisphere, from subpolar regions to the tropics (see also Nikolov and Zeller (1992)).

$$\alpha = 32.9835 - 64.884[1 - 1.3614\cos(Lat)] \tag{4.22}$$

$$\beta = 0.715 - 0.3183[1 - 1.3614\cos(Lat)] \tag{4.23}$$

$$\sigma = 0.03259 \tag{4.24}$$

Finally, a correction is applied for elevation and tilted surfaces using an exponential Beer's algorithm, where the extinction coefficient is a function of solar radiation, slope and aspects.

The resulting 1km grid surfaces of solar radiation were validated using independent real data from two meteorological stations. Figure 4.2 shows the observed and predicted mean monthly solar radiation values for the validation sites. The model showed

very good prediction over the winter and spring months, but it overestimated slightly during June, July and August for both sites. However, the difference was not statistically significant from zero for either sites ($P > 0.05$ using a two sample t-test).

4.2.2 Calibration

The calibration procedures for 3-PG are frequently manual, by adjusting a certain number of parameters to fit the patterns of observations. A detailed procedure can be found in Landsberg *et al*. (2003), which should be read together with a number of technical reports published by CSIRO (Sands, 2004), giving a detailed description of the data and the procedure needed to fit the model. Additionally Almeida *et al*. (2004) demonstrated the parameterisation procedure using series of biomass, leaf area index, litterfall, soil moisture and stomatal conductance data. Although, Landsberg *et al*. (2003) did not demonstrate parameterisation using a large dataset, the study did imply that biomass or volume data and leaf area index are needed for a proper calibration. Nevertheless, this method could be (1) problematic when the model does not fit the observations and alterations in the model procedures are needed (Landsberg *et al*., 2005) and (2) difficult for users non-familiar with the model algorithms and calibration procedures.

For both 3-PG and ICBM, the majority of the parameters have frequently come from literature, although some parameter "manipulation" is also necessary. Despite the attempts to offer a parameterisation based on real data, the uncertainty for some of the parameters, their mean values for each species and their variance with site and climatic conditions are still largely unknown. Moreover, the new 3-PGN model includes subroutines with unknown sensitivity and additional uncertainty, not only because of the new set of parameters but also because of the possible effects of the new parameters on the uncertainty of existing ones. A quantification of the uncertainty could be presented when good calibration data exist, however all previous studies have failed to do so.

An approach based on Bayesian calibration has recently been supported for forestry applications and ecological process-based models (Van Oijen *et al*., 2005). The methodology is not new in other sciences (Reckhow, 1990; Ellison, 1996, 2004), but the high

intensity of computation and the sometime cumbersome theory has discouraged its use. Moreover, the complexity of most process-based models makes it difficult to conduct an uncertainty analysis for parameters and outputs.

Bayesian calibration overcomes the above by quantifying both parameter and output uncertainty by utilising the current knowledge on the parameters' probability distribution (known as the prior probability). The probability is updated using the know distribution of the calibration data to provide the after-model posterior distribution of the parameters. Probability density functions represent graphically the uncertainty while the mean and standard deviation provide an additional quantification. The computational problem is also reduced by the use of Markov Chain Monte Carlo simulations. The produced posterior distribution of the parameter consists an uncertainty knowledge base which is updated each time new data are used. Van Oijen *et al*. (2005) brings to attention that such a knowledge base should be expanded only when the environmental conditions are the same, due to the fact that the parameter uncertainty could change.

The first demonstration of Bayesian calibration of forestry-related process-based models can be found in the early 90s (Vandervoet and Mohren, 1994). A few years later Ellison (1996), Gertner *et al*. (1999) and Radtke *et al*. (2002) demonstrated the technique once again for forest ecosystem models. The technique was previously used also for parameterising 3-PG for pine in the UK (Patenaude *et al*., 2005) providing estimates of the uncertainty and a sensitivity analysis of the parameters.

To expand the results of the previous study by including our soil sub-model, we applied Bayesian calibration to the parameter vector of 3-PGN. We produced probability density functions (pdf), their means and standard deviations for 32 parameters. We were also interested in investigating the difference in the uncertainty of the parameters with site conditions and so the model was calibrated using different data from sites across Scotland for Scots pine. More importantly, we wanted to produce a single set of parameters for Scots pine applicable for any condition across Scotland. In this regard, Bayesian calibration may not be ideal because it does not provide the "best fit" parameter set, but the one that maximizes the likelihood of producing the observed data. In other words, there could be more than one parameter vector matching the data

or it could be different vectors between sites because of an underlining relation with site factors. In any case, a set of parameter vectors representing different conditions should provide a resulting parameter set representative for the species. We included sites with as broader range of conditions and management histories as possible and we used different data sets.

Table 4.4: Upper and lower limits of the uniform prior parameter distribution.

Parameter	Upper	Lower	Reference
p_{FS_2}	1	0.4	Landsberg and Waring (1997); Landsberg *et al.* (2003)
$p_{FS_{20}}$	1	0.2	Landsberg and Waring (1997); Landsberg *et al.* (2003)
n_{Rx}	1	0.4	Waring and McDowell (2002)
n_{Rn}	0.40	0.2	Waring and McDowell (2002); Janssens *et al.* (2002)
f_{N_0}	1	0.1	-
γ_{F_x}	0.03	0.02	Schoettle and Fahey (1994); Mäkelä and Vanninen (2000); Jalkanen and Aalto (1994)
γ_{F_0}	0.0025	0.0005	-
$Rttover$	0.16	0.003	Vanninen, P. and Mäkelä, A. (2005); Mäkelä and Vanninen (2000); Janssens *et al.* (2002); Schoettle and Fahey (1994)
g_{c_x}	0.03	0.02	Beadle *et al.* (1985)
$L^*_{g_{c_x}}$	4	2.5	-
$w_{Sx_{1000}}$	600	100	-
mF	0.5	0.1	-
mR	0.5	0.1	-
mS	0.5	0.1	-
σ_0	9	4	Mencuccini and Bonosi (2001)
σ_1	6	3	Mencuccini and Bonosi (2001)
k	0.6	0.2	Law *et al.* (2000); Waring and McDowell (2002)
$fullCanAge$	25	15	-
α_x	0.06	0.03	Law *et al.* (2000); Landsberg *et al.* (2003)
Y	0.49	0.43	Waring *et al.* (1998)
ρ	0.45	0.3	-
$k_{l_{max}}$	0.1	0.009	Berg and Ekbohm (1993); Titus and Malcolm (1999); Hyvönen *et al.* (2000)
$k_{r_{max}}$	0.005	0.001	Laiho and Prescott (2004)
$k_{o_{max}}$	0.001	0.0001	Peltoniemi *et al.* (2004)
h_c	0.4	0.1	Peltoniemi *et al.* (2004)
q_{i_r}	600	90	Krankina *et al.* (1999)
q_{i_l}	60	10	Hyvönen *et al.* (2000)
q_{h_c}	50	10	Kätterer (personal comm.)
q_{b_c}	20	1	Kätterer (personal comm.)
e_l	0.6	0.1	Hart *et al.* (1994); Hyvönen *et al.* (2000)
e_r	0.6	0.1	Hart *et al.* (1994); Hyvönen *et al.* (2000)
N_{cf}	2	1	Vestgarden *et al.* (2004); Korakaki (2003)

Before carrying out the calibration procedure a literature review was conducted to summarise the values used in 3-PG for all species and especially for pine species. We identified the most sensitive parameters following the work by Esprey *et al*. (2004) and Almeida *et al*. (2004), although we also included the whole parameter set to explore the uncertainty of little-known parameters (Table 4.4). Since the most uncertain parameters were likely to be those of ICBM/2N where no previous studies existed for forest applications, the literature of similar soil model was reviewed in order to provide an indication of the range of likely values.

4.2.2.1 Bayesian calibration

Bayesian statistics require the knowledge of the uncertainty of a parameter θ to be defined by a probability distribution $P(\theta)$, more often known as prior probability. It represents the existing knowledge for the parameter. For 3-PGN parameters, no previous information exists for their distribution and as supported by Van Oijen *et al*. (2005) a uniform distribution providing maximum and minimum limits may be assumed. We obtained those values by reviewing the existing literature from studies for Scots pine, and defined the limits of the prior distribution using limits within the observed range (Table 4.4). Some parameters were kept constant, such as the maximum proportion of rainfall evaporated from the canopy, the leaf area for maximum rainfall interception, slope and intercept for net versus solar radiation relationship and conversion factor for solar radiation to photosynthetic active radiation. Soil parameters where chosen to match the soil texture conditions estimated during by an extensive field survey of the calibration sites.

The prior information was updated using the distribution of a certain dataset given a specific parameter vector, denoted as $P(Data|\theta)$. The updated information is the posterior distribution of the parameter θ given the existing data, denoted as $P(\theta|Data)$.

$$P(\theta|Data) = \frac{P(\theta)P(Data|\theta)}{P(Data)} \tag{4.25}$$

Most of the time $P(Data)$ is unnecessary to compute because of the method of computation (e.g. Metropolis-Hasting algorithm, see next section) or when the data are constant the parameter could be ignored and so $P(\theta|Data) \propto P(\theta)P(Data|\theta)$. $P(Data|\theta)$ is also known as the likelihood function of the parameter θ. To estimate the likelihood of the data given the specific model parameter vector an indication of the measurement error is needed, assuming a Gaussian function φ_g with a mean of zero and a give standard deviation (SD, Equation 4.26)

$$P(Data|\theta) = \prod_{i}^{n} \varphi_g(Data_i - f_i(\theta); 0, SD_i) \tag{4.26}$$

where, n is the number of data points used and $f_i(\theta)$ is the model's output. In our case n differed from site to site depending on the number of available data. Because no information about the distribution of the data was available we assumed a constant standard deviation of 5 t/ha for biomass and 5 $\mathrm{m}^3\ \mathrm{ha}^{-1}$ for stand volume.

4.2.2.2 Markov Chain Monte Carlo simulation and Metropolis-Hastings algorithm

Applying Bayes' theorem to a model with analytically solved equations is relatively straightforward, as long as the prior distribution is also simple. However, in the case of a process-based model this rapidly becomes extremely difficult. In the case of 3-PGN we needed to explore a 32-dimensional parameter space. Monte Carlo simulations provide the tool to randomly select and evaluate a parameter vector from the prior distribution. However, a completely random sampling from a large parameter space is highly computational intensive especially when a large number of iterations is needed until the Markov chain "burns in" (Van Oijen *et al*., 2005). Moreover, each parameter vector has to be evaluated by estimating the likelihood.

To speed up the computation time, we adopted the Metropolis-Hastings algorithm for Markov Chain Monte Carlo (MCMC) as it was described by Van Oijen *et al*. (2005) and Robert and Casella (2004). The algorithm provides a random walk through the

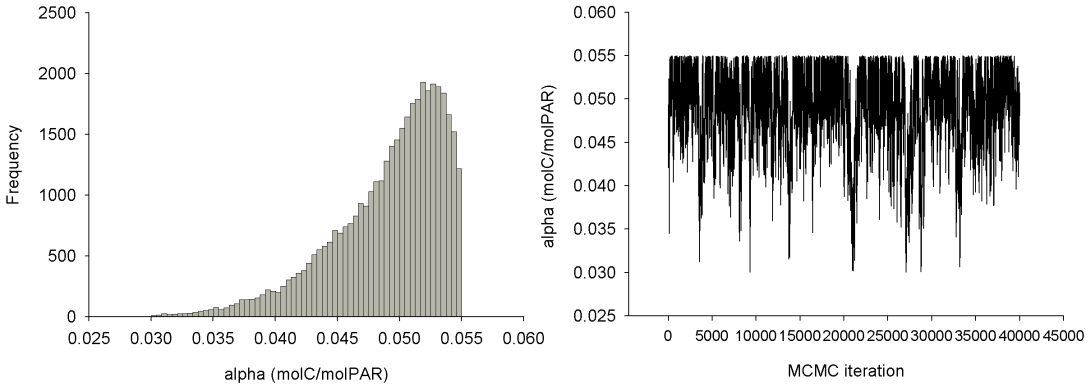

Figure 4.3: Posterior distribution for maximum quantum yield efficiency (Site 1) and Markov Chain Monte Carlo trace plot.

parameter space by satisfying certain criteria. First a new value of the parameter θ' is set using the previous value $\theta' = \theta_t + \epsilon$, where ϵ is a random vector derived from a Gaussian distribution with a mean of zero and a SD set to 5% for the majority of the parameters.

$$\beta = \frac{P(\theta'|Data)}{P(\theta_t|Data)} = \frac{P(Data|\theta')P(\theta')}{P(Data|\theta_t)P(\theta_t)} \tag{4.27}$$

Using the new value, the ratio β is estimated and compared with a random variable u derived from a uniform distribution (0,1). When $u \leq \beta$ then the proposed value θ' is accepted and $\theta_{t+1} = \theta'$ otherwise $\theta_{t+1} = \theta_t$. If $\beta \geq 1$, that is, the posterior value of the new parameter is larger than the posterior value of the previous parameter, the proposed value θ' is always accepted. With this algorithm a sample from the parameter space is chosen carefully and could be considered as a representative sample of the posterior distribution.

4.2.2.3 Calibration and validation procedure

Our calibration procedure had two objectives. First, to quantify uncertainty of 3-PGN's parameters and second, to provide a parameter set representative to of the climate and site conditions of Scots pine commercial stands. Additionally, we wanted to deter-

mine the differences in the uncertainty by comparing the Bayesian calibration results between sites.

The first part was achieved by running MCMC for six sites across Scotland using the PSP data. Each site was run for 40,000 iterations, this being a sufficient number to allow the chain to "burn in". This could be verified by visually inspecting Markov Chain Monte Carlo trace plots (Figure 4.3). The posterior distributions for the 32 parameters was estimated for each site together with some of the major outputs of the model, such as stem biomass and stand volume. Climatic inputs were extracted from the spatial database whereas initial values for 3-PGN's state variables such as biomass of foliage, roots and stems were set as 0.01, 0.1 and 0.1 respectively (Forestry Commission, Forest Management Tables, 1966). Soil state variables were also considered following a steady state condition (Peltoniemi *et al.*, 2004). Soil texture information was used to estimate soil water retention parameters from our field survey and maximum soil water capacity was assumed constant at 300mm (Waring, 2000). The number of observation data varied depending on availability.

The difficulty however lies with our second objective. Because Bayesian calibration does not present the "best fit" parameters but the "most likely" to occur given a certain data set, so we devised a strategy to include the variability of parameter set with site conditions. To do so, we ran another set of MCMC for eight sites across Scotland from our second dataset (Table 4.3). We extracted the "most likely" parameter vectors for the eight sites and also for the initial six PSP sites used to quantify uncertainty. Then, we estimated means and standard deviation for each parameter from the total fourteen sites and the coefficient of variation (CV) was calculated. Parameters with a CV under the threshold of 20% were considered as not having great variance among sites and the mean value was used in subsequently. The parameters with a CV exceeding the threshold were used for further MCMC simulations. The size of the vector was thus reduced by fourteen parameters. The parameters not greatly varying across sites included σ_0, σ_1, α_x, Y, k, $fullCanAge$, f_{N_0}, $p_{FS_{20}}$, n_{Rx} and N_{c_f} (see also Table 4.2 for values). Before proceeding, the resulting parameter vector was compared with an independent validation PSP data set, for stands with different initial stocking and with

no thinning regimes. Since the fit was not good, we proceeded with several cycles of Bayesian calibration. To reduce the computation time of this process, we reduced the number of PSP calibration sites to three. After the simulation the "most likely" parameter vector for the three sites was extracted and averaged. The CV was checked and the set was tested again against the observed data. If the fit was still not good, some parameters were manually changed to give reasonable fits based on the literature data for pine species. This process was repeated five times by progressively reducing the size of the parameter vector and increasing the goodness of fit against the PSP validation sites, to end up with a parameter set which we consider the best for the different growing conditions of Scots pine. The resulting parameter vector was finally validated using the same PSP validation dataset, which includes eight plots with different initial stocking and without any thinning regimes.

4.2.3 Sensitivity analysis

We also performed a sensitivity analysis to identify the effect of each parameter on the outputs of both 3-PG and ICBM/2N, Patenaude *et al*. (2005, and personal communication) used the resulting posterior distributions to produce partial correlation coefficients between the parameters and the model outputs and among the parameters. This methodology provides useful information for the relationships of the parameters with the model's outputs, although it has the limitation of assuming linearity. For our model such information is unknown. Additionally, because of the lack of posterior information for the main soil carbon outputs and the desire to quantify the likely effect of a parameter's change to the outputs of 3-PGN, we performed a sensitivity analysis based on the technique presented by Esprey *et al*. (2004). This method allows to explore the likely effect of each parameter on the main outputs of both 3-PG and ICBM/2N and to explore any non-linear relationship between parameters and outputs.

$$\lambda_1(X,p) = \frac{p}{X}\frac{\partial X}{\partial p} \tag{4.28}$$

$$\lambda_2(X,p) = \frac{p^2}{X}\frac{\partial^2 X}{\partial p^2} \tag{4.29}$$

We run the model on a monthly time step, for a specific site, varying the parameter values and the soil state variables by 10% and 40% either side. We explored the major outputs of the model including tree and soil carbon pools, stand volume, litter and leaf area index and finally nitrogen availability and uptake. We estimated the relative sensitivity and the relative non-linearity of a certain output X to a parameter or input p with Equations 4.28 and 4.29 respectively, for each point in time and averaged the values for the whole simulation period. Greater values indicated higher sensitivity or non-linearity. The analysis did not include differences in sensitivity across sites. The parameter vector used for the analysis included the eleven parameters of the soil sub-model and all the major parameters of 3-PG, including biomass partitioning, leaf area estimation, temperature modifiers and initial values of maximum soil water availability and soil carbon pools.

Table 4.5: Coefficients of determinations (R^2) and slope for the comparison between predicted (x axis) and observed (y axis) values of stem number (N, ha^{-1}), stand volume (V, $\mathrm{m}^3\ \mathrm{ha}^{-1}$), mean diameter at breast height (D, cm), aboveground tree biomass (W_{AB}, tDMha^{-1}) and stem biomass (W_S, tDMha^{-1}) for the eight PSP validation plots. Regression line was forced through origin. Number in brackets indicate the initial planting density.

	Plot 1 (12346)		Plot 2 (12346)		Plot 3 (5102)		Plot 4 (5102)	
	R^2	slope	R^2	slope	R^2	slope	R^2	slope
N	0.63	0.96	0.86	1.11	0.75	0.56	0.99	1.04
V	0.97	0.88	0.95	0.83	0.84	1.09	0.74	0.94
D	0.87	0.85	0.88	0.77	0.98	1.14	0.98	0.91
W_{AB}	0.89	1.15	0.91	0.94	0.92	1.34	0.78	1.17
W_S	0.77	0.86	0.81	0.70	0.95	0.94	0.93	0.84
	Plot 5 (5102)		Plot 6 (3086)		Plot 7 (1736)		Plot 8 (1736)	
	R^2	slope	R^2	slope	R^2	slope	R^2	slope
N	0.79	0.77	—	—	—	—	—	—
V	0.94	1.02	0.88	0.73	0.89	0.71	0.92	0.65
D	0.88	0.93	0.76	0.83	0.87	0.72	0.82	0.87
W_{AB}	0.99	1.16	0.93	0.93	0.94	0.86	0.98	0.89
W_S	0.99	0.85	0.96	0.68	0.97	0.63	0.98	0.64

4.3 Results

4.3.1 Performance of 3-PGN

The performance of 3-PGN was tested using some of the major outputs of the model, such as aboveground and stem biomass, stand volume, diameter at breast height and total number of stems per hectare. However, no soil data were available for comparison. Table 4.5 illustrates the coefficients of determination and the slopes of the relations between model predictions and observations for the eight validation plots (see also Figure 4.4).

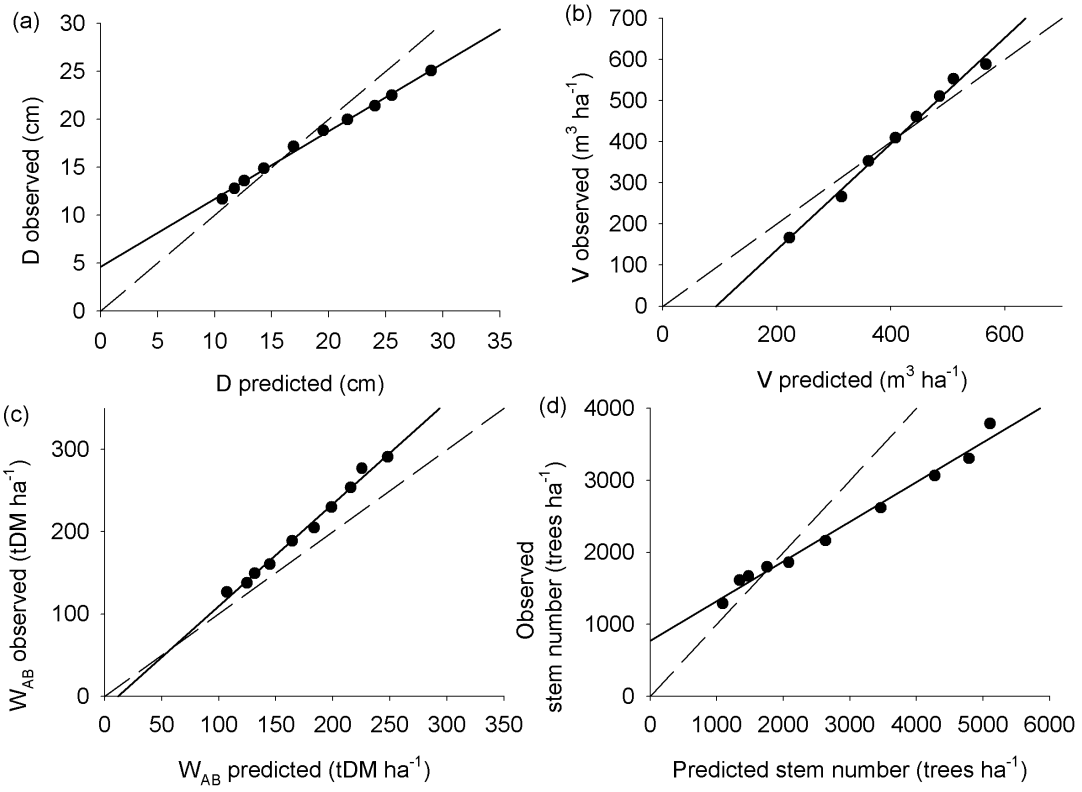

Figure 4.4: Predicted against observed values of (a) mean diameter at breast height (D, cm), (b) stand volume (V, $\mathrm{m}^3\ \mathrm{ha}^{-1}$), (c) aboveground biomass (W_{AB}, $\mathrm{tDM\ ha}^{-1}$) and (d) stand density ($\mathrm{trees\,ha}^{-1}$) for one of the validation plots. Plot belongs to the network of permanent sample plot established by Forestry Commission. Dashed line represents 1:1 relationship.

The model successfully predicted the patterns of stand volume, diameter and above ground biomass for stands starting with a very high planting density. However, stem number and stem biomass were not adequately predicted ($R^2 = 0.63$ and $R^2 = 0.77$

respectively) for plot 1, while values for plot 2 were slightly better. When stands with a medium planting density were simulated the predictions were clearly improved except for stem number.

However, when stands with a low initial planting density were simulated the model failed to adequately reproduce stem numbers pattern. Interestingly, predictions for stand volume and stem biomass gave a high coefficient of determination but the slope was much lower than the slope for mean diameter and above ground biomass for plots 6, 7 and 8. The model's failure to reproduce stem number or stem biomass successfully in stands with low planting density probably indicates that foliage biomass is overestimated while stem biomass is underestimated. A representative example is given in Table 4.8, where in the stands planted with low densities, small percentages of self-thinning are observed at young age resulting to a smooth rate of decrease in stem number, whereas 3-PGN applies greater self-thinning intensities, particularly when stands are older.

4.3.2 Uncertainty

To summarize the uncertainty of the parameter vector from the posterior distributions of each parameter we calculated the mean vector and coefficient of variation matrix for each of the six sites. Additionally, we produced pdf graphs for each parameter (Figures 4.5, 4.6 and 4.7, pages 129, 130 and 131 respectively) to explore graphically within-sites and between-sites uncertainty. We also estimated the mean of the "most likely" parameters, the mean coefficients of variation and standard deviations for the the six sites as indicator of the between-site uncertainty (Figure 4.8 and Table 4.6).

Table 4.6 shows high uncertainty for $Rttover$ at all of the six sites. Site 1 has the highest uncertainty with 76.8% variation and a mean value of 0.055, whereas site 2 has a variation of 57.6% and a mean value of 0.067. Overall the mean coefficient of variation for this parameter between sites is 61.0% with a mean of 0.070. On the other hand the ratio between P_N and P_G seems to be the least uncertain parameter within site, whilst also not variable across sites. Site 1 has the lowest uncertainty with 2.4%

Table 4.6: Descriptive statistics for the posterior distribution of the 32 parameters of 3-PGN estimated for each of the six uncertainty sites. Mean coefficients of variation and standard deviations for the six sites were also estimated as indicators of the variation of the parameters between sites.

Parameter	Site 1		Site 2		Site 3		Site 4		Site 5		Site 6		$\overline{\Theta}$	$\overline{\mathrm{CV}}$	$SD_{\overline{\mathrm{CV}}}$
	$\overline{\theta}$	CV	$\overline{\theta}$	CV	$\overline{\theta}$	CV	$\overline{\theta}$	CV	$\overline{\theta}$	CV	$\overline{\theta}$	CV			
p_{FS_2}	0.714	22.9%	0.778	18.4%	0.759	20.1%	0.770	20.0%	0.760	20.3%	0.755	20.1%	0.756	20.3%	1.5%
$p_{FS_{20}}$	0.689	30.3%	0.660	33.7%	0.648	35.0%	0.624	35.5%	0.574	38.9%	0.672	31.7%	0.644	34.2%	3.0%
n_{Rx}	0.506	15.6%	0.515	15.5%	0.566	18.1%	0.528	16.2%	0.529	17.2%	0.555	17.8%	0.533	16.7%	1.1%
n_{Rn}	0.303	18.6%	0.284	19.0%	0.296	19.1%	0.289	18.7%	0.300	18.7%	0.289	19.6%	0.294	18.9%	0.4%
f_{N_0}	0.694	10.9%	0.682	12.1%	0.620	18.7%	0.642	15.9%	0.633	17.2%	0.653	15.0%	0.654	15.0%	3.0%
γ_{F_x}	0.024	11.1%	0.024	11.0%	0.024	11.3%	0.025	11.6%	0.025	11.4%	0.024	11.2%	0.024	11.3%	0.2%
γ_{F_0}	0.002	36.2%	0.002	38.6%	0.001	39.5%	0.002	34.9%	0.002	38.3%	0.001	38.7%	0.001	37.7%	1.7%
$Rttover$	0.055	76.8%	0.067	57.6%	0.070	61.0%	0.069	61.8%	0.094	41.6%	0.066	67.2%	0.070	61.0%	11.6%
g_{c_x}	0.025	11.0%	0.025	11.1%	0.025	10.9%	0.025	11.0%	0.025	11.3%	0.025	11.1%	0.025	11.1%	0.1%
$L^*_{g_{c_x}}$	3.330	12.2%	3.340	12.1%	3.288	12.8%	3.284	12.1%	3.308	12.5%	3.269	12.6%	3.303	12.4%	0.3%
$w_{Sx_{1000}}$	285.597	23.9%	130.624	16.9%	186.028	31.4%	581.591	42.6%	136.508	23.9%	200.739	40.8%	253.514	29.9%	10.2%
mF	0.307	37.1%	0.287	39.0%	0.291	37.0%	0.291	38.0%	0.287	38.8%	0.299	37.8%	0.294	37.9%	0.8%
mR	0.318	34.4%	0.311	35.6%	0.289	38.9%	0.289	37.4%	0.292	36.6%	0.295	36.8%	0.299	36.6%	1.5%
mS	0.329	33.0%	0.380	23.9%	0.338	30.6%	0.302	35.2%	0.333	30.4%	0.326	33.5%	0.335	31.1%	4.0%
σ_0	6.722	21.2%	7.166	17.9%	6.616	20.8%	6.729	20.4%	6.499	20.8%	6.685	20.7%	6.736	20.3%	1.2%
σ_1	4.892	15.2%	4.939	14.9%	4.878	15.3%	4.865	15.3%	4.766	16.5%	4.847	16.4%	4.865	15.6%	0.7%
k	0.504	13.6%	0.515	12.5%	0.488	17.3%	0.490	16.0%	0.481	17.4%	0.484	16.8%	0.494	15.6%	2.1%
$fullCanAge$	18.232	12.7%	16.985	9.5%	18.052	12.1%	19.307	14.1%	19.169	13.5%	19.760	13.9%	18.584	12.6%	1.7%
α_x	0.049	9.1%	0.049	9.2%	0.046	13.6%	0.046	13.2%	0.045	14.3%	0.047	12.3%	0.047	12.0%	2.2%
Y	0.451	2.4%	0.474	4.5%	0.474	4.8%	0.473	4.7%	0.474	4.7%	0.473	4.6%	0.470	4.3%	0.9%
ρ	0.374	11.4%	0.380	10.8%	0.377	10.9%	0.378	11.2%	0.369	11.6%	0.408	7.7%	0.381	10.6%	1.4%
$k_{l_{max}}$	0.057	43.9%	0.057	43.5%	0.056	46.3%	0.056	44.7%	0.056	44.2%	0.054	46.3%	0.056	44.8%	1.2%
$k_{r_{max}}$	0.003	37.7%	0.003	37.8%	0.003	35.8%	0.003	35.6%	0.003	38.3%	0.003	34.4%	0.003	36.6%	1.6%
$k_{o_{max}}$	0.001	47.7%	0.001	40.0%	0.001	47.0%	0.001	48.8%	0.001	42.3%	0.001	45.0%	0.001	45.2%	3.4%
h_c	0.255	32.9%	0.250	33.2%	0.242	33.9%	0.248	33.7%	0.259	31.6%	0.251	31.9%	0.251	32.9%	0.9%
q_{i_r}	337.143	42.1%	348.165	40.8%	360.892	38.1%	336.738	41.8%	356.428	39.3%	343.231	41.8%	347.099	40.7%	1.6%
q_{i_l}	33.712	41.7%	32.765	42.0%	34.166	40.1%	35.179	39.8%	33.682	41.2%	36.008	37.9%	34.252	40.4%	1.5%
q_{h_c}	30.816	36.4%	28.818	38.6%	29.131	38.1%	30.688	37.0%	31.113	34.6%	30.733	37.3%	30.217	37.0%	1.4%
q_{b_c}	10.221	51.1%	11.182	46.4%	11.274	45.4%	10.510	48.6%	11.537	45.0%	11.503	43.5%	11.038	46.7%	2.7%
e_l	0.354	39.4%	0.319	42.1%	0.355	39.6%	0.363	37.0%	0.368	38.6%	0.360	38.6%	0.353	39.2%	1.7%
e_r	0.358	40.8%	0.364	37.9%	0.353	39.9%	0.344	40.6%	0.367	37.9%	0.352	38.9%	0.356	39.3%	1.3%
N_{c_f}	1.447	19.1%	1.484	19.0%	1.507	18.6%	1.503	18.8%	1.488	18.4%	1.524	18.3%	1.492	18.7%	0.3%

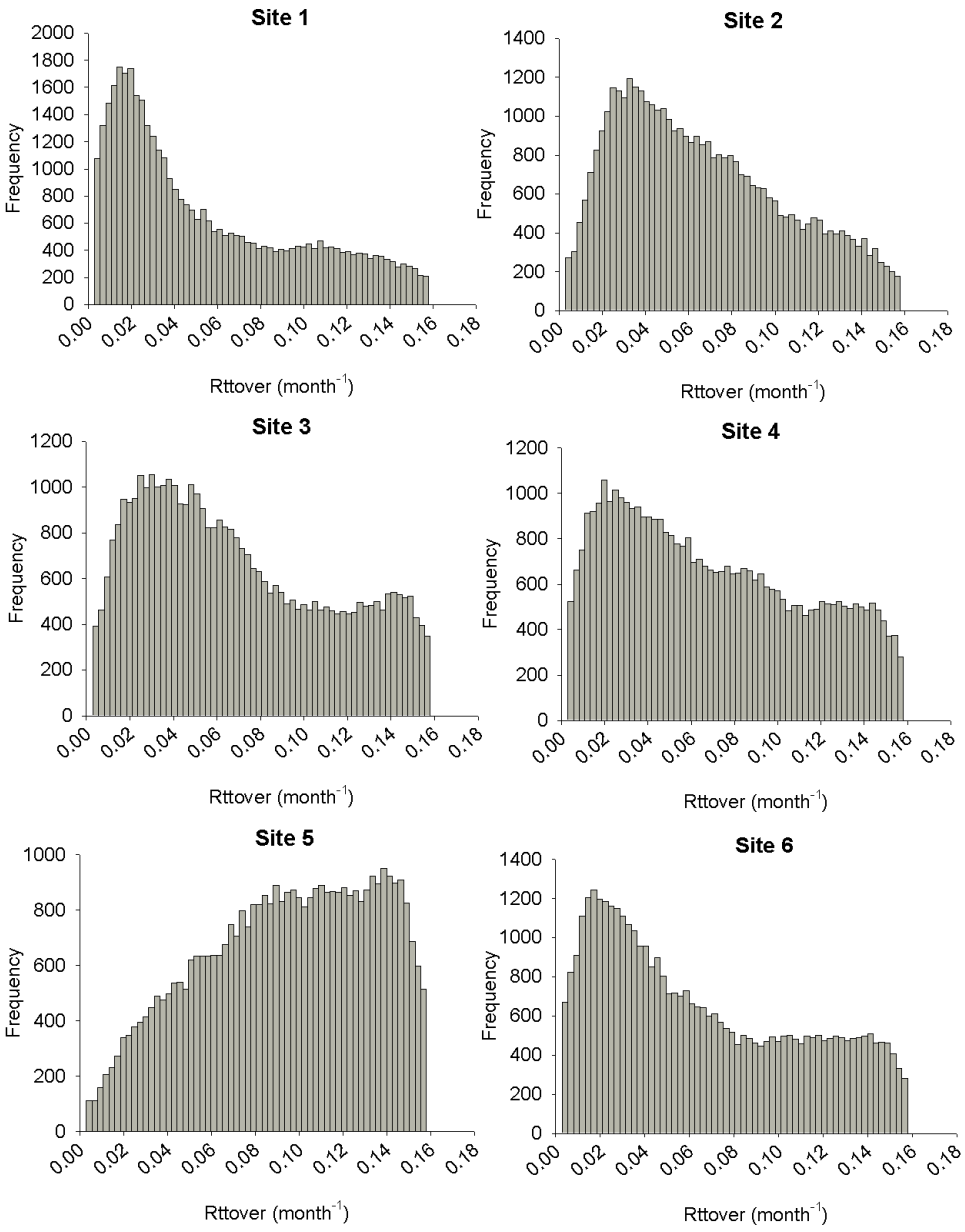

Figure 4.5: Posterior distributions for root turnover rate for the six uncertainty sites. The difference in the shape of the distribution indicates a difference in the most likely values for which the model fits the observations, which is most likely to be due to differences in site characteristics such as soil texture, moisture and density.

and a mean of 0.451, whereas site 3 has the highest variation of 4.8% with a mean 0.474. Nevertheless, the variation between sites is still very low at 4.3%. $w_{Sx_{1000}}$ is also highly uncertain with site 2 having a CV of 16.9% and a mean of 130.624, wheras site 4 has a CV of 42.6% with a mean of 581.591.

While a few of 3-PG parameters appear to have high uncertainty, high uncertainty

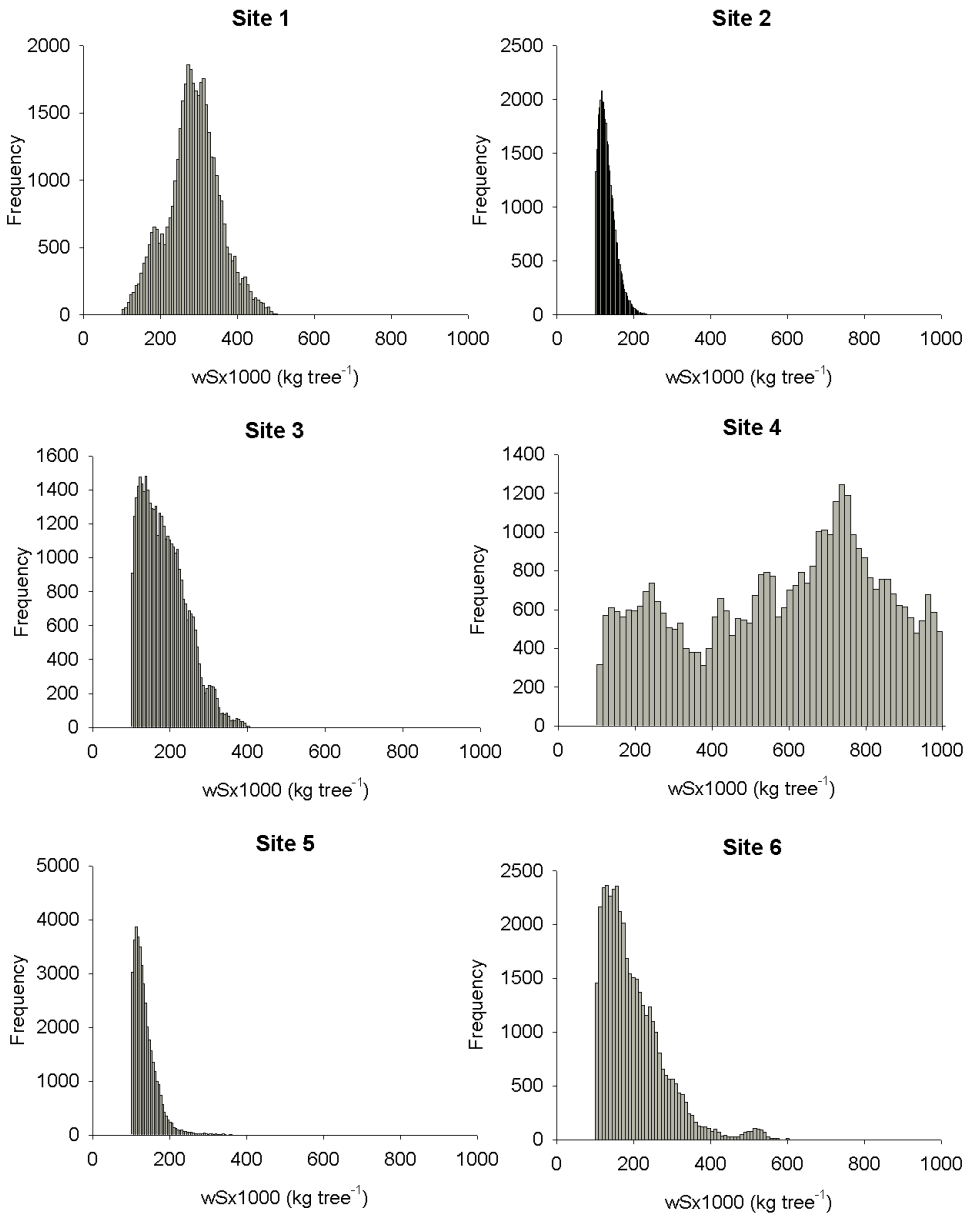

Figure 4.6: Posterior distribution for the maximum stem biomass per tree at 1000 trees per hectare for the six uncertainty sites. Again we see that variable shapes indicate the most likely values differ for each site.

is also associated with ICBM/2N parameters. Some of the most uncertain ones are q_{b_c}, and all three decomposition rates $k_{l_{max}}$, $k_{r_{max}}$ and $k_{o_{max}}$. All of the soil carbon parameters have an uncertainty of more than 30%. This could be interpreted as a result of the difference in environmental conditions (including temperature, water and soil type effects) as there is a probability that different conditions could produce the same output. It must also be considered that the lack of any soil carbon data during the

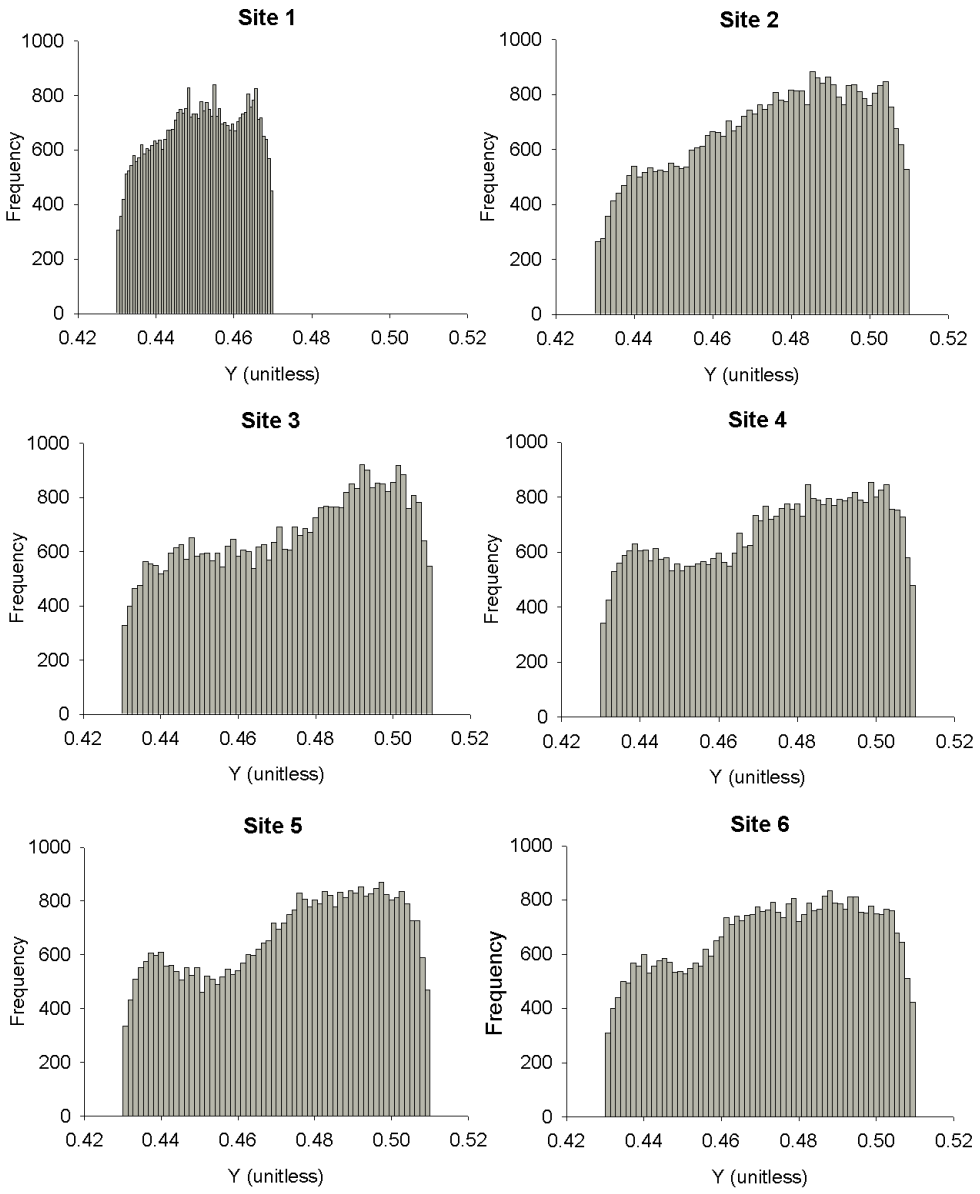

Figure 4.7: Posterior distribution for the ratio between net and gross primary production. The shape of the distribution for each site is quite similar, supporting the assumption that this ratio is similar for the species independent of location.

calibration procedure increased the uncertainty of the parameters. However, most of the soil parameters appear not 'to be very different between sites, except from the $k_{o_{max}}$ and q_{b_c}.

Microbial activity of both young pools on the other hand, together with their respective C:N ratios, had a coefficient of variation around 40%. Parameters such as the

fractions of foliage, stem and root biomass lost for each single tree removed (mF, mS and mR respectively) have mean values around 0.3 with a CV of about 30 to 35% across sites. The light extiction coefficient (k) showed a smaller uncertainty with values ranging from 0.480 for site 5 to 0.515 for site 2 and with a CV as high as 17.4%. The foliage:stem partitioning ratio at a diameter of 20 cm also exceeded the thershold of 30%. Additionally, parameters related to stand condition at the initial stage, e.g., σ_0 and γ_{F_0} have high uncertainty (Table 4.6). Finally, the quantum yield effieciency ranged from 0.0449 for site 5 to 0.0491 for site 1 with a CV lower than 15% for all sites.

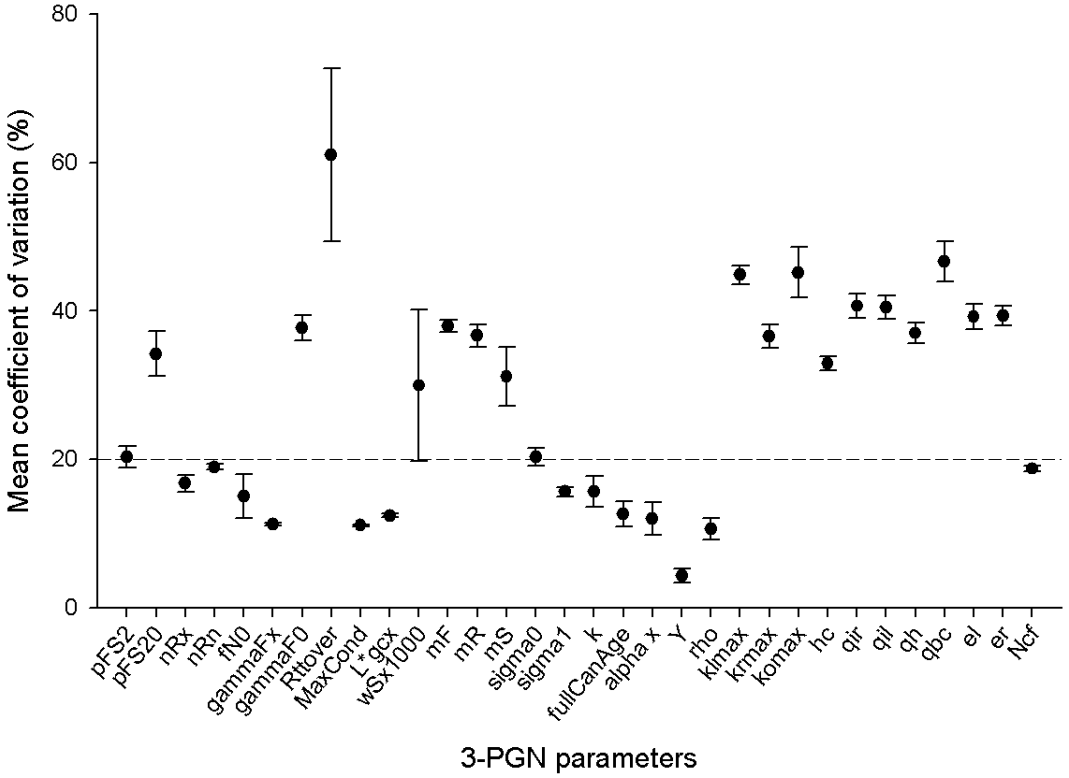

Figure 4.8: Mean coefficient of variation ($\overline{\mathrm{CV}}$) for the 32 parameters of 3-PGN estimated from the six uncertainty sites (see also table 4.6). Bars represent standard deviation ($\mathrm{SD}_{\overline{\mathrm{CV}}}$) of the estimation.

The less uncertain parameters also included n_{Rx}, n_{Rn} f_{N_0}, γ_{F_x}, g_{c_x}, $L^*_{g_{c_x}}$, σ_1, $fullCanAge$ and ρ, all of which having a CV lower than 20% at each site (Figure 4.8).

4.3.3 Sensitivity analysis and non-linearity

A thorough investigation was conducted on the relationships between parameters and outputs of 3-PGN and the most important results for some of the major outputs are given here. Figure 4.9 illustrates the effect of 3-PG parameters on soil carbon stocks and nitrogen availability and uptake, while Figure 4.10 shows the effects of ICBM/2N parameters on biomass predictions. Table 4.9 summarises the results of the first comprehensive sensitivity analysis of ICBM/2N.

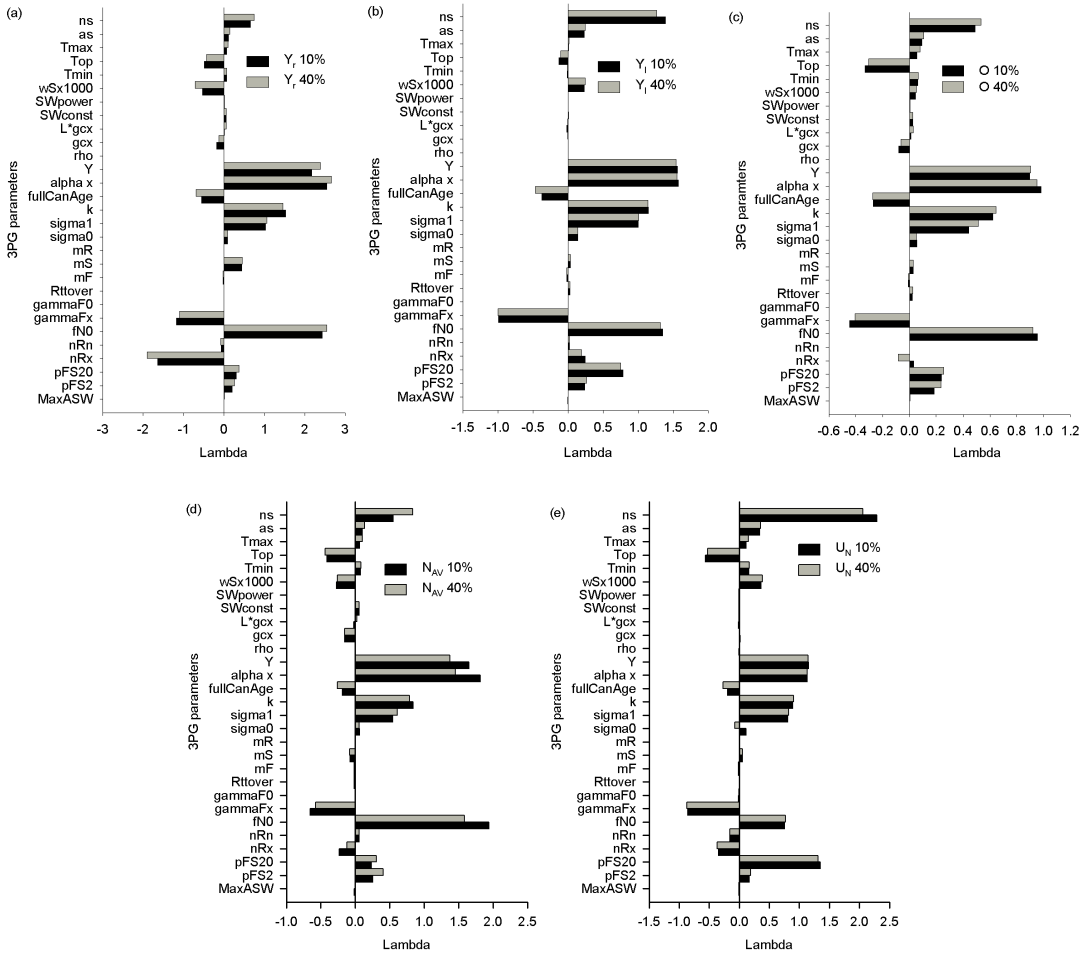

Figure 4.9: Sensitivity (λ_1) of (a) young labile, (b) young refractory, (c) old soil carbon stocks, (d) nitrogen availability and (d) nitrogen uptake to the 3-PG parameter vector for a change of 10% and 40%.

Our results indicate that biomass predictions of 3-PGN is not affected by changes in the soil sub-model parameters (Figure 4.10), although a strong non-linearity existed (Figure 4.11). Non-linearity in most occasions seems to be high with a 10% change of

the parameters but it disapears when the change became larger (40%) and that is the case for the majority of the outputs (Figures 4.11 and 4.12).

Young and labile carbon stocks were found to be highly sensitive to Y, α_x, k, σ_1, f_{N_0}, $p_{FS_{20}}$, n_s and γ_{F_x}. Young and refractory carbon stocks on the other hand were highly sensitive to Y, α_x, k, σ_1, $fullCanAge$, f_{N_0}, n_s, n_{Rx}, γ_{F_x}, T_{opt} and $w_{Sx_{1000}}$. Humified carbon was also sensitive to the same parameter set. Nitrogen availability was highly sensitive to Y, α_x, k, f_{N_0}, n_s, and γ_{F_x}, while nitrogen uptake was sensitive to a similar parameter set including $p_{FS_{20}}$. Root turnover rate appeared to have no effect on carbon or nitrogen stock. We also found that parameters to which 3-PGN was sensitive to (e.g. Y and α_x) are also those with the lowest uncertainty in their estimations. Conversely, root turnover, whose values were very uncertain appeared to have non significant effect on model's predictions.

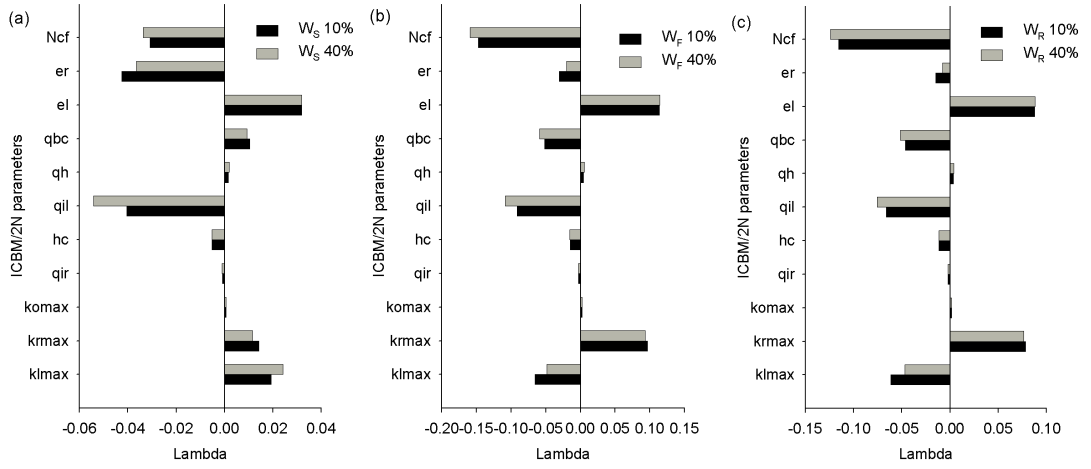

Figure 4.10: Sensitivity (λ_1) of (a) stem, (b) foliage and (c) root biomass to the ICBM/2N parameter vector for a change of 10% and 40%.

From the analysis performed between the parameters and the outputs of each model we found that nitrogen availability was highly sensitive to $k_{l_{max}}$, q_{b_c} and e_l, while nitrogen uptake was sensitive only to N_{c_f}. Finally, the sensitivity analysis of 3-PG's outputs on model parameters showed that stem biomass was sensitive to n_{Rx}, γ_{F_x}, $fullCanAge$, T_{opt}, f_{N_0}, σ_1, k, α_x and Y.

On the other hand foliage biomass is sensitive to γ_{F_x}, $p_{FS_{20}}$, f_{N_0}, σ_1, k, α_x, Y and n_s. Finally, root biomass was sensitive to γ_{F_x}, $Rttover$, $p_{FS_{20}}$, n_{Rx}, f_{N_0}, σ_1, k, α_x, Y and

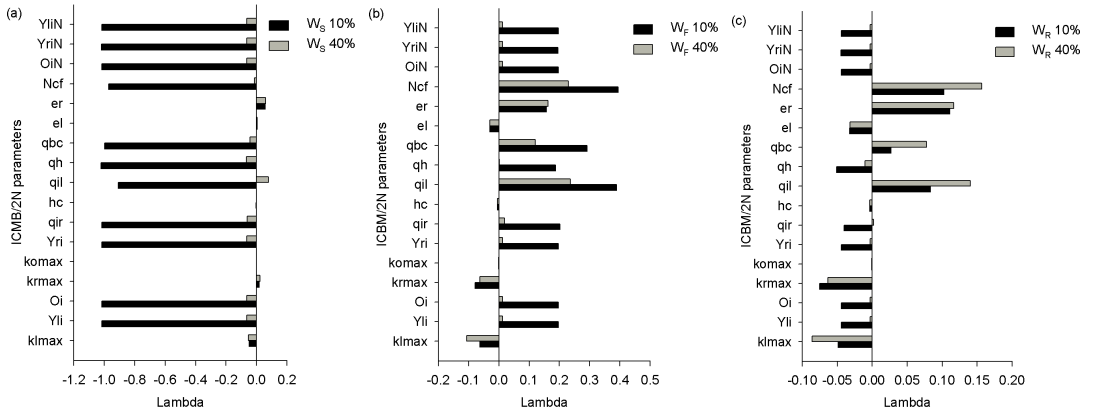

Figure 4.11: Non-linearity (λ_2) of (a) stem, (b) foliage and (c) root biomass with the ICBM/2N parameters for a change of 10% and 40%.

n_s. Non-linearity again was an issue, observing similar extreme variations between small and large changes in the parameter's value (data not shown), especially with some of the ICBM/2N parameters and initial state variables.

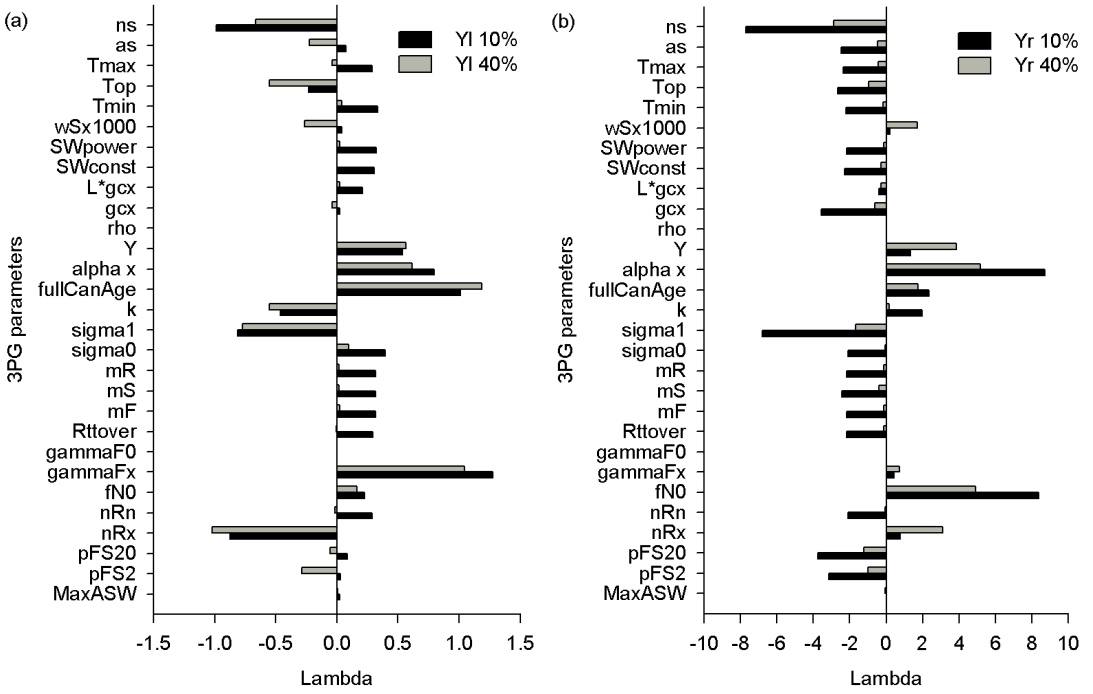

Figure 4.12: Non-linearity (λ_2) of (a) young labile, (b) young refractory carbon pools, (c) nitrogen availability and (d) nitrogen uptake with the 3-PG parameters for a change of 10% and 40%.

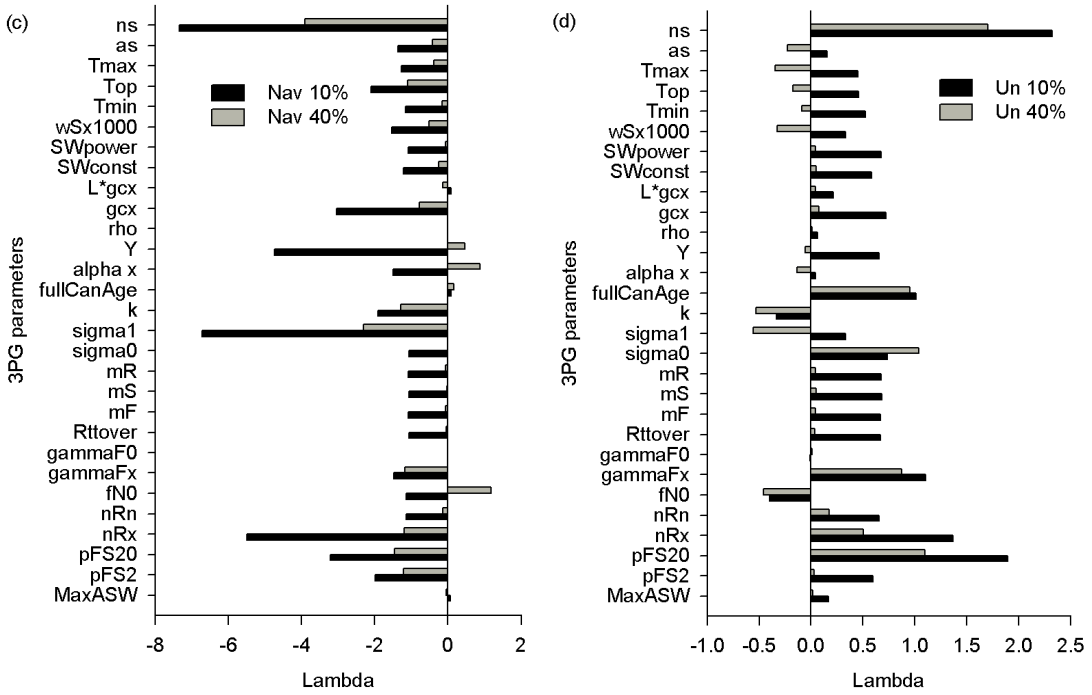

Figure 4.12: *Continued*

4.4 Discussion

Our study represents the first attempt to parameterise the complete ecosystem model 3-PGN and is only the second parameterisation of 3-PG for Scots pine. Our results showed that 3-PGN can reliably represent patterns of stand volume, aboveground and stem biomass and diameter at breast height. Our success however was compromised by the not so successful matching of foliage and root biomass. With regard to this aspect, we are unable to reach any safe conclusions on the model's performance as our foliage and root "observations" were estimated from allometric relationships with breast diameter. A more complete parameterisation of 3-PGN needs to include a calibration data set with information about foliage and root biomass, carbon and nitrogen stocks in a chronosequence and nitrogen availability.

The validation process also showed that 3-PGN had a problem in predicting reliable stem number patterns for stands with low initial planting density. To understand a bit more of why this might have happened we conducted a more careful analysis of

the patterns of a stand development of our PSP validation plots. According to Westoby (1984), the self-thinning rule can be explained by using the graph of logarithm of biomass per unit area ($\log_{10}B$) versus the logarithm of density of the survival population ($\log_{10}N$), as described by Equation 4.30.

$$\log_{10}B = \log_{10}C - \frac{1}{2}\log_{10}N \tag{4.30}$$

where C is the intercept of the power function. In this expression of the self-thinning rule, the thinning line has a slope of -1/2 indicating the line passed which natural mortality occurs. When this relationship is expressed in terms of the logarithm of the mean biomass of the surviving trees and the logarithm of the population density of the surviving trees, then this slope becomes -3/2. This rule is well established across species and it is known to be affected by site fertility and intensity of shading (Westoby, 1984). We estimated the slope and the intercept of Equation 4.30 for the eight validation plots using both observations and model results of stem biomass and number of trees per hectare.

Table 4.7: Self-thinning slopes and intercepts from Equation 4.30 as it was estimated from observation data and from 3-PGN for different stocking densities. Time series data for stem biomass and stocking were used for each of the eight validation plots.

		Observations		3-PGN	
Plot	Initial stocking	Slope	Intercept	Slope	Intercept
1	12346	-0.485	3.839	-0.500	3.906
2	12346	-0.473	3.729	-0.500	3.906
3	5102	-0.778	4.628	-0.500	3.906
4	5102	-0.656	4.332	-0.500	3.906
5	5102	-0.794	4.788	-0.535	4.020
6	3086	-1.783	7.860	-0.592	4.189
7	1736	-1.184	6.051	-0.825	4.873
8	1736	-2.646	10.224	-1.011	5.447

Table 4.7 shows that the self thinning slope for stands where the initial planting density was very high it was very close to the theoretical value (≈ -0.5). However, when stand

development started with a density less than 5000 stem per hectare, the slope of the self-thinning line increased reaching values of up to -2.6. On the other hand, 3-PGN gives exactly the theoretical value of the slope for high density stands, but it shows only a very small increase when the planting density becomes very low. What is clear from this exercise is that stands with low initial planting density do not follow the theoretical self-thinning law during much of their development (Table 4.8) because there is less competition for nutrients and light and mortality is low. We believe that 3-PG's failure to match the observed stem number for plots 6-8 was because of this difference in the relationship between biomass and density, which was unable to capture.

Table 4.8: Observed values (Obs.) of number of stems per hectare predicted by 3-PGN, and the percentage of tree mean reduction ($\overline{red}$) for two of the calibration plots (6 and 8). It is clear that the model does not follow the slope of self-thinning observed in reality. Both plots show a very slow rate of decline in tree numbers, while 3-PGN does not apply any thinning in the early stages of a stands life but suppresses trees rapidly when they get older.

Plot 6					Plot 8				
Stand Age	Obs.	$\overline{red}$ (%)	3-PGN	$\overline{red}$ (%)	Stand Age	Obs.	$\overline{red}$ (%)	3-PGN	$\overline{red}$ (%)
29	2270		3086		27	1379		1736	
35	2170	4	2820	9	34	1334	3	1736	0
40	1982	9	2161	23	38	1294	3	1736	0
46	1778	10	1656	23	41	1275	1	1736	0
50	1607	10	1422	14	47	1215	5	1530	12
55	1493	7	1203	15	51	1146	6	1325	13
62	1419	5	989	18	56	1097	4	1134	14
67	1387	2	880	11	62	1028	6	971	14
					67	1018	1	873	10

The results from the first sensitivity analysis performed on ICBM/2N showed the importance of labile and refractory decomposition rates on the prediction of carbon accumulation (Table 4.9) with both of these rates showing an inverse relationship with the size of young pools, indicating an increase in the amount of nitrogen and carbon stored in the soil with decreasing decomposition. Young carbon pools represent the first decomposition stage where the input litter is starting to decompose. However, these chemically unstable pools will increase the respiration losses as the process of decomposition is increased and carbon is lost. On the other hand, the old pool represent the more stable carbon storage where carbon is "locked" and so respiratory losses are much lower. Microbial activity also affects the nitrogen stocks, as it helps the break

down of complex substances (e.g., lignin) into simpler, easily available by trees forms such as nitrate and ammonium. The process was successfully captured by the model as microbial activity (e_l) increases nitrogen stocks and availability. The model also

Table 4.9: Results of the first sensitivity analysis performed on the ICBM/2N model. Only highly significant results are presented ($|\lambda_1| \geq 0.5$)

Parameter	Y_{N_l}		Y_{N_r}		Y_l		Y_r	
	10%	40%	10%	40%	10%	40%	10%	40%
$k_{l_{max}}$	-0.798	-0.895	—	—	-0.976	-1.124	—	—
$k_{r_{max}}$	—	—	—	—	—	—	-0.543	-0.570
h_c	—	—	—	—	—	—	—	—
q_{b_c}	-0.808	-0.956	-0.928	-1.098	—	—	—	—
e_l	0.820	0.821	—	—	—	—	—	—
e_r	—	—	1.282	1.336	—	—	—	—
N_{c_f}	—	—	—	—	—	—	—	—
Parameter	O		N_{AV}		U_N			
	10%	40%	10%	40%	10%	40%		
$k_{l_{max}}$	—	—	-0.736	-0.565	—	—		
$k_{r_{max}}$	—	—	—	—	—	—		
h_c	0.586	0.586	—	—	—	—		
q_{b_c}	—	—	-1.003	-1.167	—	—		
e_l	—	—	1.000	0.997	—	—		
e_r	—	—	—	—	—	—		
N_{c_f}	—	—	—	—	0.832	0.839		

showed that nitrogen coming from the fast decomposition of foliage and roots is the most important pool influencing the availability and of course the fertility of the site. The limit of this approach is that the model does not explicitly represent the difference in decomposition between fine and coarse root with the amount of carbon entering the labile pool including both coarse and fine roots, causing a slight overestimation of the input carbon. A correction could be applied by separating the input root biomass into a labile and a refractory pool by using constant ratio. Nevertheless, because death of roots (Figure 4.9) does not significantly affect either carbon or nitrogen stocks, thus such correction would not improve any prediction.

The rest of our sensitivity analysis results came in good agreement with those from previous studies performed on 3-PG (Almeida *et al.*, 2004; Esprey *et al.*, 2004). We also found that Y, $p_{FS_{20}}$, α_x, n_{Rx}, f_{N_0} and T_{opt} are important not only for biomass but for

stand volume too (data not shown) and Y, $p_{FS_{20}}$, γ_{F_x}, σ_1 and α_x for L^* (Esprey *et al.*, 2004), however we could not find any significance of g_{c_x} on any of the outputs. Root turnover was found to affect only root biomass to which it is directly linked. Interestingly, we did not find any relationship between root turnover and soil carbon storage, a result also observed by Paul *et al.* (2003a) in his evaluation of 3-PG with the integrated GRC3 model. The optimum temperature for growth as well as the rate of uptake of nitrogen affects stem and root biomass growth the most (Figure 4.9). Temperature can limit photosynthesis as high air temperatures will increase vapour pressure deficit and cause the stomata to close which stops growth and of course uptake of nitrogen. Specific leaf area was also proved to be significant for soil carbon accumulation, as it affects foliage biomass production and so litter input, matching again the observations by Paul *et al.* (2003a). One of the most important 3-PG parameters is also f_{N_0}, which appears to effect almost every output. Because of the way FR has been modelled, the possibility of getting a value of zero indicating a nutrient limitation at that precise time of stand's development has increased, the accurate estimation of f_{N_0} has become increasingly important and so the calibration data should provide information of the fertility of the stand at the time of nutritional stress. Finally once more we have seen that the proportion of gross primary production turned into net production, although it reduces the complexity of the modelling still consists a parameter which should be carefully chosen.

Highly encouraging was the fact that ICBM/2N did not change the internal relationships between 3-PG's parameters and its outputs, as it caused no effect on productivity (Figure 4.10). A similar result was observed before in a recent integration of 3-PG with Roth-C model (Hirsch *et al.*, 2004). The sensitivity analysis showed a non-significant effect of the soil model for ecosystem carbon storage. The authors concluded that the combination of the fast turnover rates and of a small carbon flux passed to the soil pools resulted in the carbon storage being very small, which could also be the case with our model. On the other hand, we have seen a more direct effect of 3-PG parameters on the soil outputs. Parameters relating to allometry such as $p_{FS_{20}}$ and n_s and those related to canopy development such as σ_1 and γ_{F_x} showed a great effect on the development of soil carbon and nitrogen stocks as they were directly linked to the litterfall inputs.

Comparing our parameter vector with that used by Landsberg *et al*. (2005) for Scots pine stands in Finland, we find that in both studies well established physiological parameters were used for Scots pine such as maximum canopy conductance with a value of 0.02 $\mathrm{m\ sec^{-1}}$ (Beadle *et al*., 1985), while leaf area index for maximum canopy conductance was 3.33 and boundary layer conductance 0.2 $\mathrm{m\ sec^{-1}}$ (Beadle *et al*., 1985). Our results came in good agreement for parameters such as the ratio of net and gross primary production (Waring *et al*., 1998; Landsberg *et al*., 2003), f_{N_0}, γ_{F_x} and $Rttover$. Also the constant and the power of the stem allometric relation derived from our pooled regression were close to the values used by the same study. However, we also identified differences for important parameters such as maximum stand age used in the age modifier, the power of relative age, the relative age to given $f_{AGE} = 0.5$ and specific leaf area. The first three parameters were fitted to match age related decline of productivity observed by Magnani *et al*. (2000). We also used a specific leaf area for seedlings of 6 $\mathrm{m^2\ kg^{-1}}$ and 4 $\mathrm{m^2\ kg^{-1}}$ for mature leaves (Mencuccini and Bonosi, 2001) while Landsberg *et al*. (2005) uses 9 and 6 respectively. Mencuccini and Bonosi (2001) for the same latitude as the sites used by Landsberg *et al*. (2005) give a projected leaf area of 5.5 $\mathrm{m^2\ kg^{-1}}$. A possible explanation was given by Duursma *et al*. (2004) who applied for coniferous species a modification in foliage allocation to account for seasonality, by assuming that leave grow in one month in the spring and abscise one month in the autumn. In any other case where this seasonality is absent then probably higher values of specific leaf area are needed. An other explanation could be the differences we found in light extinction coefficient. Our value of 0.5 is in contrast with the value of 0.6 used by Landsberg *et al*. (2005), meaning that less light penetrates the canopy of Finish stands, which might be due to high density planting. This forces the leaves to expand their area as there is a strong competition for light. Photosynthesis of Finish stand is more efficient as quantum yield efficiency is larger however its fast rates could make the carbohydrate allocation less efficient and so decrease the weight of leaves. That will result in high values of specific leaf area. Our value of 0.05 is slightly lower than the "universal" value for pine species of 0.055 (Landsberg *et al*., 2003) by Landsberg *et al*. (2005). Thus could be due to the relationship of quantum efficiency with soil fertility, as our stands grow on sandy, podzolic and podzolic brown

earth soils.

In Figure 4.8 and Table 4.6 we demonstrated the uncertainty associated with the prediction of 3-PGN parameters as estimated by our Bayesian calibration procedure. The results showed that the most uncertain parameters, such as $Rttover$, mS, mF, mR and ten out of eleven soil parameters are those showing the least sensitivity to the productivity outputs. This makes their use more reliable even when their values are not very representative. On the other hand, important parameters such as Y come with the lowest uncertainty and a well defined range of likelihood (Figure 4.7). However, we observed extreme non-linear relations between most of the parameters and outputs of the model (Figures 4.11 and 4.12). Non-linear relations should be considered carefully as they can hide potential high sensitivity (Esprey *et al.*, 2004). An interesting pattern observed was the disappearance of the strong non-linearity when the change of the parameter was 40%. If we assume that λ_2 is the second order derivative of the parameter's relation with a certain output and a linear relationship exists between the 10 and 40% change of the parameter, this will have as a result a third degree polynomial relationship for the parameter, which could possible lead to an exrtreme response of the output when a change occurs. Figure 4.8 and Table 4.6 also illustrate the uncertainty between the six calibration sites. By assuming that for a parameter to be the same across sites its posterior distribution should be similar, we found that $Rttover$ is the most uncertain parameter between sites. Root turnover is not a species-specific parameter, as it can depend on several environmental factors, such as soil temperature, microbial activity, water-logging, frost or nutritional status which could differ between sites. As Figure 4.5 illustrates, that could cause the mean to shift from the less fertile site 1 (low root turnover means more roots and thus greater need for nutrients) to the more fertile site 5 (high root turnover means small proportion of root biomass and thus less need for nutrients). On the other hand, for the foliage:stem ratio at a diameter of 20cm on the other hand, the differences between sites were smaller but potentially still quite significant. It is an allometric parameter greatly affecting the outputs of foliage biomass, leaf area index, nitrogen availability and uptake as well as litterfall and nitrogen and carbon pools. This parameter could be affected by many environmental factors such as fertility, light or VPD. Fertile sites will have bigger $p_{FS_{20}}$, as they will have greater

supply of nutrient and so greater photosynthetic capabilities. VPD could also effect the allocation to foliage as demonstrated by the reported ranges in leaf-sapwood area ratios in Scots pine with varying VPD (Mencuccini and Grace, 1996; Mencuccini and Bonosi, 2001). $w_{Sx_{1000}}$, $k_{o_{max}}$, q_{b_c}, f_{N_0} and mS are parameters whose values could be variable across different sites depending on the local environemntal conditions and thus they should be considered carefully if a parameter vector is to be used across sites.

Although we did not include the state variables of soil carbon and nitrogen in our uncertainty analysis we estimate their sensitivity. We found limited or no sensitivity of tree outputs to the initial values of soil carbon and nitrogen pools, although highly non-linear relations was found for both small and large change.

Bayesian calibration is a statistical methodology producing more trustworthy results. However, there are several elements which need to be considered before its use, which potentially could lead to wrong conclusions. First is the prior distribution. In our case study no information was available on the prior distribution of the parameters and so a uniform distribution was assumed. It is important though to consider any prior knowledge of the parameters or the outputs. In our case, information from the literature review was considered as prior knowledge of the limits of the uniform distribution. Since the uncertainty was expected to be very high and no previous information existed, the choice of the parameters limits must be more relaxed. A second potential problem was the lack of data for some components of the model, particularly the soil dynamics sub-model. The lack of data becomes crucial when relationships between parameters and model outputs exist that are not obvious. The estimation of the soil parameters from entirely productivity outputs is one such example in which an "added" uncertainty is created because of the indirect link between parameters and outputs. In such a case a sensitivity analysis may provide an indication of whether an underlining relationship exists but was not defined. On the other hand, Bayesian calibration is applicable even with a small dataset and provides a broad knowledge of the parameters and outputs uncertainty, which would normally be impossible with a manual calibration. Also, automated methods are certainly more efficient in choosing parameters for models with large parameter vectors. Finally, it must be remembered that it does not provide the

user with the ”optimum fit”. Devising a calibration strategy such as the one presented, whereas several cycles of Bayesian calibration are applied for a number of sites across a region can provide a mean parameter vector applicable to all situations.

The modelling of the new fertility rating removes the uncertainty deriving from the estimation of the parameter by the user based on the results of a soil survey. The new approach makes FR not a direct indication of site fertility or a way to classify it but an internal parameter providing the necessary indication of the current nutritional status of the stand and how it will effect future production (i.e., it becomes a ”fertility indicator”). As such, comparisons across sites based on this new FR may not be valid. However, the range of values take by FR and the time during which these values occur can allow to compare between sites. Additionally, site classification may now be based upon a larger number of variables, including soil carbon and nitrogen stocks or potential primary production or sequestered carbon. This criteria may provide an alternative to the classical site index used by forest managers for site classification. Although the need for manual adjustment of site fertility is no longer present, FR now comes with its own uncertainty, and the number of parameters for calibration has increased. Despite this, those values can be more easily estimated by collection of soil samples and the laboratory estimation of carbon and nitrogen stocks and the decomposition rates of various pools of soil organic matter. A further investigation on the relationships between parameters and outputs and on the representation of the major processes in the model would provide a more thorough understanding of the model outputs.

4.5 Conclusions

In this paper we carried out a comprehensive investigation of the newly proposed integration of the simplified process model ICBM/2N with the routines of 3-PG. Our objective of removing the manual adjustment of 3-PG's fertility rating was achieved by introducing a small number of new parameters. This has brought new uncertainty on the model's predictions and the need for a better understanding of the internal feed-

backs. The simplicity of ICBM/2N matches the philosophy of 3-PG to provide a simplified process-based model based on fundamental eco-physiological functions. Our implementation of the newly proposed technique of Bayesian calibration for ecological models provided us with information about the uncertainty of parameters and also an automated procedure for calibration. We found that 3-PGN realistically predicts the productivity patterns of Scots pine stands across Scotland. A complete calibration dataset, including a soil carbon stock chronosequence is required to improve the parameterisation.

Root turnover rates were proven to be the most uncertain parameter, while the ratio of net and gross primary production was the least uncertain. Fortunately, the most uncertain parameters had minor effect on productivity. The most significant parameters included the quantum yield efficiency, f_{N_0}, σ_1, and allometric parameters such as $p_{FS_{20}}$ and n_s. There was no significant effect of the soil sub-model on the major outputs of 3-PG (timber volume and stand biomass) however, found significant non-linear relationships with soil initial state variables for a small change of the parameter, which could potentially lead to high output sensitivity. Through our validation procedure we identified the weakness of 3-PG's self-thinning algorithm when the initial planting densities were very low.

The results of the Bayesian calibration for eight sites showed that some parameters are likely site-specific, probably because of some underlining relationships with site factors. Their use for predicting productivity at different sites or for spatial simulations should be considered carefully. Finally we showed that Bayesian calibration of ecological models is a very useful tool for understanding the relationships between parameters and outputs of a model. However, certain pitfalls could easily lead to wrong conclusions. A prior knowledge of parameters' distribution was found very significant for the procedure to be applicable. When a uniform distribution is chosen for parameters with no previous prior knowledge, the choice of the upper and lower limits should be wide enough to provide sufficient exploration of their uncertainty.

CHAPTER 5

Assessing spatial and temporal patterns of productivity and yield of Scots pine across Scotland using 3-PGN SPATIAL

5.1 Introduction

At the dawn of the 21th century forests are proven to be extremely valuable for human kind. Apart from being the main contributor to the world's oxygen supply, forests provide a wide range of products and services, whose significance we probably started to appreciate fully only in the first quarter of the 20th century. However, the last few decades have seen their multi-purpose role highlighted even more as their distribution across the globe started to decline. In addition to several other functions, a new role was established for forests with the adoption of the Kyoto protocol as unique carbon stores and sinks, which can contribute significantly in the reduction of atmospheric carbon content. This multi-purpose role is illustrated in the recent Scottish Forestry Strategy with its primary vision to make *"Scotland's trees, woodlands and forests the central part of the country's culture, environment and economy"* (Forestry Commission, Scottish Forestry Strategy, 2006). Amongst other objectives of the strategy is to *"enhance opportunities for health and enjoyment, through access and recreation, contribute to growth in learning and skills, develop a more efficient and competitive timber supply chain, increase the contribution of forestry to tourism, support the development of markets for forest products, help to tackle climate change, help to protect and enhance biodiversity, contribute positively to soil, water and air quality, and contribute*

to landscape quality" (Forestry Commission, Scottish Forestry Strategy, 2006). Meeting the objectives of such a strategy demands fast, accurate, reliable and easy access to information for forest managers, through a competent network of decision support systems (DSS) based on modern technology.

Certain aspects of current forest management (such as rotation length, thinning regimes, etc.) are still quite heavily determined by the objective of maximizing timber production. Traditionally, forestry decisions are based on information supplied by a well established methodology of site classification based on yield and mean annual increment (e.g., yield tables, yield classes and site indices). Such methodologies are capable of ensuring sustainability of a maximum yield, a constant annual income from extracted timber, and the continued existence of the current forest distribution of species and age. However, when it comes to meeting carbon sequestration objectives for climate change mitigation, current methodologies fail to provide reliable information regarding relevant forest ecosystem attributes.

A range of methodologies can provide estimates of ecosystem carbon sequestration. They include field measurements of annual net primary production (e.g., Ovington, 1957; Albrektson, 1980; Vanninen *et al.*, 1996; Oleksyn *et al.*, 1999, 2000; Vucetich *et al.*, 2000; Gower *et al.*, 2001; Xiao *et al.*, 2003, 2004; Zianis and Mencuccini, 2005), eddy covariance measurements of net ecosystem production (Markkanen *et al.*, 2001; Kolari *et al.*, 2004; Wang *et al.*, 2004a), biomass expansion factors to convert forest inventory data to carbon stocks coupled with inventory data for soil carbon stocks(Brown *et al.*, 1999; Lehtonen *et al.*, 2004; Levy *et al.*, 2004; Lehtonen, 2005), remote sensing data at a regional (Jiang *et al.*, 1999; Mickler *et al.*, 2002a,b; Hörsch, 2003; Zheng *et al.*, 2004) or global scale (Field *et al.*, 1995; Prince and Goward, 1995), modelling estimation in a stand (Waring, 2000; Grant, 2004; Landsberg *et al.*, 2005; Bugg *et al.*, 2006, see also Chapter 6), regional (Coops and Waring, 2001; Coops *et al.*, 2001b; Tickle *et al.*, 2001a,b; Zuo *et al.*, 2003; Swenson *et al.*, 2005) or global scale (Foley, 1994; Cao *et al.*, 1996), modelling based on remote sensing data at a regional (Coops *et al.*, 1998; Coops and Waring, 2001; Coops *et al.*, 2001b; Swenson *et al.*, 2005) and global scales (Liu *et al.*, 1997) and modelling utilising spatially interpolated data un-

der a Geographical Information System (GIS) framework (Cannell and Milne, 1995; Ditzer *et al*., 2000; Kimball *et al*., 2000; Tickle *et al*., 2001a,b; Tan and Shibasaki, 2003; Zuo *et al*., 2003; Seidl *et al*., 2005; Swenson *et al*., 2005; Bugg *et al*., 2006).

Spatial modelling provides a range of tools for obtaining reliable regional and national scale patterns of forest productivity. Integration of process-based models with GIS (Ditzer *et al*., 2000; Kimball *et al*., 2000; Tickle *et al*., 2001a,b; Tan and Shibasaki, 2003) provides a mapping tool for visualisation of current and future forest productivity, although this for the vast majority of models failed to include both aspects of production in terms of volume increment and carbon sequestration. 3-PG SPATIAL (Tickle *et al*., 2001a,b) is a simplified process-based model which fills this gap, being capable of providing spatial prediction of mean annual volume increment and stand volume. Also, recent model development (Chapters 4 and 6) made 3-PG a complete ecosystem model capable of predicting soil decomposition and soil carbon stocks, while also providing information on soil nutritional status.

3-PG is a well established model simulating forest production based on basic physiological principles of growth. It has been applied successfully in a wide range of biomes and climatic conditions including *Eucalyptus* plantations (Coops *et al*., 1998; Tickle *et al*., 2001a; Sands and Landsberg, 2002), Rimu (*Dacrydium cupressinum* Solander ex G. Forst., White *et al*., 2000; Whitehead *et al*., 2002), tropical species of the Amazon basin (Hirsch *et al*., 2003, 2004; Stape *et al*., 2004) and many conifer species such as *Pinus patula* Schlecht. and Chamisso (Dye, 2001), Sitka spruce (Waring, 2000) and most recently Scots pine in Finland (Landsberg *et al*., 2005). Tickle *et al*. (2001a,b), Landsberg *et al*. (2003) and Coops *et al*. (1998); Coops and Waring (2001); Coops *et al*. (2001b) demonstrate application of 3-PG in a regional scale utilising spatial data derived from remote sensing and Geographical Information Systems (GIS). It has been successfully integrated with many other process-based models (Liu *et al*., 2002; Peng *et al*., 2002; Zuo *et al*., 2003; Hirsch *et al*., 2004; Paul and Polglase, 2004; Sampson *et al*., 2006), while Landsberg *et al*. (2003),Whitehead *et al*. (2002) and Law *et al*. (2001) used 3-PG to reduce the gap between flux measurements with eddy covariance techniques and process-based ecosystem models. Law *et al*. (2000) compared 3-PG

with Pnet-II in an investigation of water vapour exchange and productivity of ponderosa pine, while Waring (2000) investigated the environmental limitations of Sitka spruce growth in Great Britain. Landsberg *et al*. (2005) also demonstrated the effects of long term management on the accumulation of biomass and stem size distribution of Scots pine in Finland. Finally, Duursma *et al*. (2004) introduced a relatively simple canopy photosynthesis sub-model, which was applied in a mixed-species conifer forest on complex terrain. 3-PG has also been integrated with forest patch-models such as PICUS (Seidl *et al*., 2005) and GROWEST (Zuo *et al*., 2003). The latest applications of 3-PG come with an investigation on the effects fertility on forest carbon storage after an integration with the process-based model SECRETS (Sampson *et al*., 2006), the prediction of site index across Oregon in USA using 3-PG SPATIAL (Swenson *et al*., 2005) and simulation of tree growth in Australia in point and spatial mode (Bugg *et al*., 2006). Evaluation of the model (Landsberg *et al*., 2003; Sands and Landsberg, 2002) and sensitivity analysis of parameters and output variables (Almeida *et al*., 2004; Esprey *et al*., 2004, see also Chapter 4 of this thesis) provided a better understanding of the internal feedbacks of the model, whereas modern computation techniques such as Markov Chain Monte Carlo simulations demonstrated a new method for model parameterisation and the exploration of the parameters' uncertainty (Chapter 4; Patenaude *et al*., 2005).

Site classification on the other hand, has never been derived based on carbon sequestration potentials. Although all process-based models produce high quality easy stem-related variables, they have not been used to provide a site classification scheme. Sequentially, efforts in the UK and elsewhere have been made to provide a site classification incorporating climatic and site effects, such as temperature, wind forces and soil nutritional and moisture status (Ecological Site Classification (ESC), Pyatt *et al*., 2001; Ray, 2001).

In this paper, we demonstrate the application of the process-based model 3-PGN and of its spatial version to estimate the potential productivity patterns of Scots pine in Scotland. We used 3-PGN SPATIAL to explore the temporal changes and the spatial patterns of productivity and to determine the major physiological variables and

environmental factors affecting Scots pine growth. Additionally, we demonstrate the potential of a site classification scheme based on ecosystem carbon accumulation as well as timber production.

5.2 Material and methods

5.2.1 The 3-PGN SPATIAL model

3-PGN, and its spatial version 3-PGN SPATIAL, is a full ecosystem model, integrating in a two-way dynamic coupling two simplified process-based model, 3-PG (Landsberg and Waring, 1997) and ICBM/2N (Andrén and Kätterer, 1997). 3-PG is a well established process-based model (Landsberg *et al*., 2003). As explained in Chapter 4, the new model maintains all the existing algorithms of 3-PG, while it introduces a new way of estimating site fertility and its effect on production based on the decomposition of existing carbon and nitrogen pools (Chapter 4). 3-PGN SPATIAL is a modification of the stand alone application of 3-PG SPATIAL (Tickle *et al*., 2001a,b) and 3-PGS Coops *et al*. (1998), which was developed after customizing and recompiling the existing C++ source code to provide a loose coupling between the model and the ArcInfo GIS workstation. 3-PGN SPATIAL utilises spatially interpolated weather and soil inputs with the possibility of incorporating also satellite inputs of NDVI, to provide spatially and temporally explicit predictions of variables such as mean breast height diameter, stem, foliage and root biomass, net primary production, soil carbon and nitrogen stocks and fluxes. The model is driven by a series of climatic and soil inputs, including mean monthly minimum and maximum temperature, precipitation, incoming solar radiation, frost days and soil class, which in 3-PGN SPATIAL could be either unique values or spatially interpolated grids. The model also includes a series of initial state variables including stem, foliage and root biomass, labile, refractory and old carbon and nitrogen pools, available soil water and latitude, with again the option of spatial inputs. 3-PGN SPATIAL was calibrated and validated for monospecies, even-aged plantation of Scots pine in Scotland using Bayesian calibration (Van Oijen *et al*., 2005) by running consecutive Monte Carlo Markov Chains for a range of Scots pine plots across a latitude

and elevation range. A more complete description of the model structure is provided in Chapter 4.

5.2.2 Data sources

5.2.2.1 Weather data

Climatic data were obtained from the Climate Research Unit of the University of East Anglia (CRU), in a regular 10 km point grid for the period 1961 - 1997 for the whole of Great Britain. The data set included values of mean monthly maximum and minimum temperature (°C), mean monthly precipitation (mm), mean monthly vapour pressure deficit (mBar), rain days, frost days and air humidity (%).The data set was geostatistically interpolated in 1 km grids and then reduced to a distribution covering Scotland's mainland (Figure 5.1).

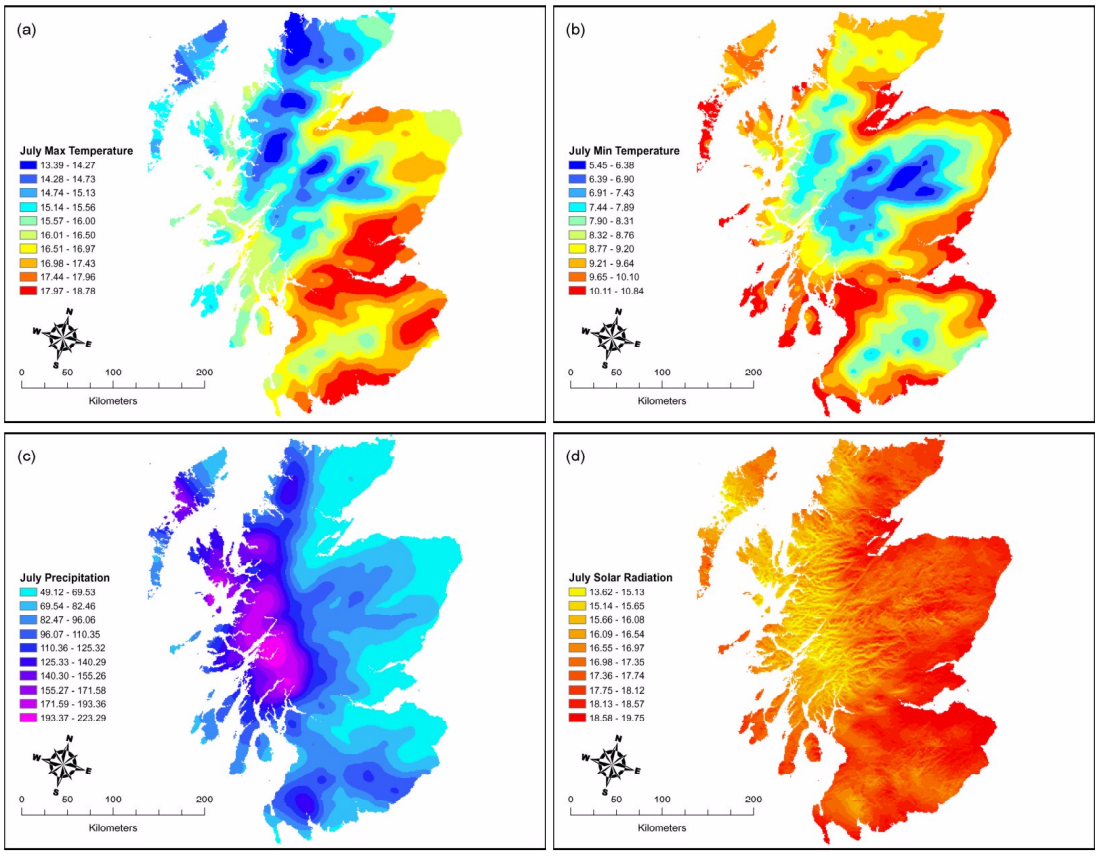

Figure 5.1: Surfaces for July's (a) maximum temperature (°C), (b) minimum temperature (°C), (c) precipitation (mm), and (d) incoming solar radiation (MJ m^{-2} day^{-1}).

5.2.2.2 Elevation and Latitude

A 50m resolution Digital Elevation Model (DEM) was obtained by Ordnance Survey UK. Resolution was reduced to 1 km using a bilinear interpolation algorithm within ArcInfo workstation. The produced DEM was used for prediction of incoming solar radiation. Weather data from CRU provided also information about latitude, which were then interpolated using geostatistics from the 10 km point grid to 1 km surface (Figure 5.2).

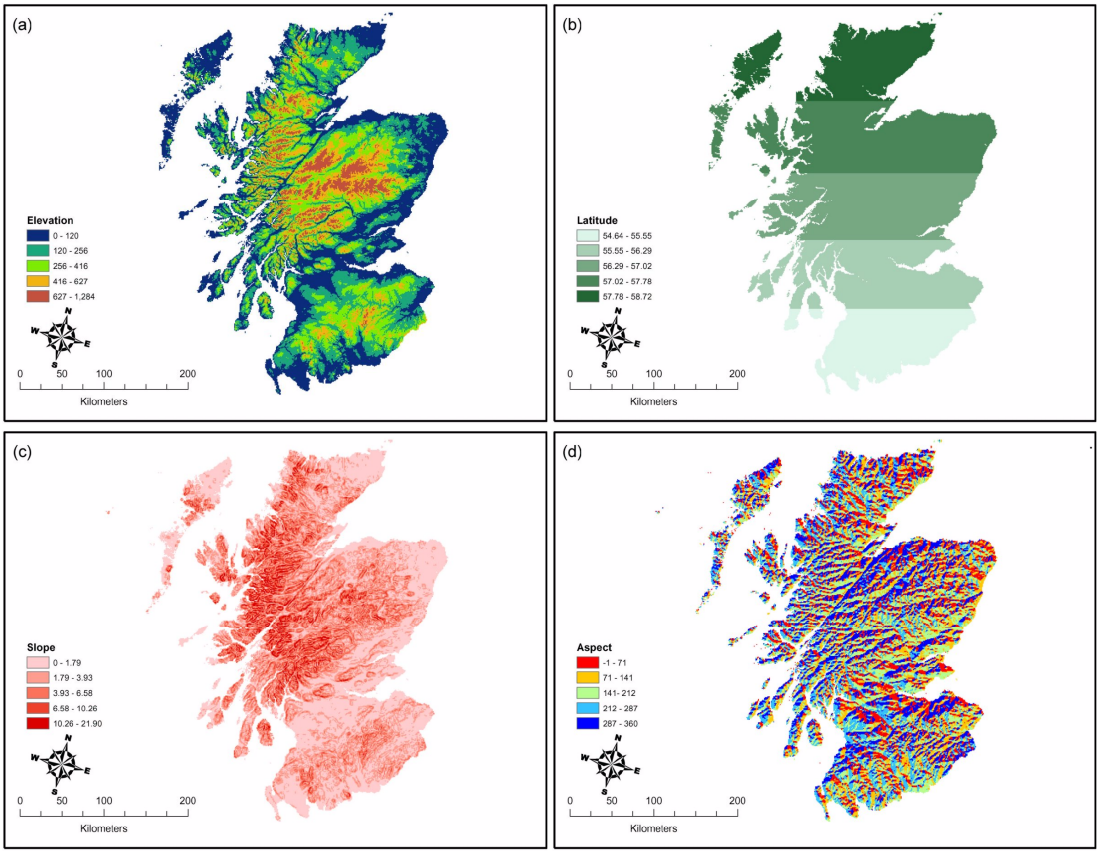

Figure 5.2: Maps of (a) elevation (m), (b) latitude (decimal degrees), (c) slope (degrees) and (d) aspect (degrees) for Scotland. Latitude surface was interpolated from CRU data, whereas slope and aspects were produced from a Digital Elevation Model (DEM) by Ordnance Survey.

5.2.2.3 Solar radiation

Incoming solar radiation is a key driving factor for 3-PGN, thus accurate predictions are vital to successful modelling. There are several approaches to produce spatial sur-

faces of solar radiation for local and national scale predictions, including transmitivity (Coops *et al*., 2000; Waring, 2000), clear-sky transmittance (Thornton and Running, 1999; Thornton *et al*., 2000), process-based analyses using calculations of sun angle, latitude, slope and aspects and weather corrections (Swift, 1976; Brock, 1981), geostatistical analyses that spatially interpolate data from weather stations, when a good network exists (Rehman and Ghori, 2000), or lately artificial neural networks (Mohandes *et al*., 1998; Antonic *et al*., 2001; Dorvlo *et al*., 2002).

Surfaces of global incoming solar radiation for Scotland were developed using a semi-empirical model (Nikolov and Zeller, 1992) applied within ArcInfo workstation, utilising surfaces of mean monthly temperature, precipitation, humidity, cloudiness and latitude. Corrections for topography and altitude were based on the produced 1 km DEM.

The structure of the algorithm is simple. First it estimates the incoming solar radiation on the top of the atmosphere depended on the Julian day, solar declination, solar sunrise/sunset hours and latitude. Then the amount of solar radiation is estimated on the earth's surface by reducing the mean monthly amounts of solar radiation on the top of the atmosphere by a non-linear proportions of cloudiness. The cloudiness is estimated by mean monthly water vapour pressure and total precipitation. Mean monthly water vapour pressure is estimated using an exponential relationship with relative humidity and mean monthly temperature. The empirical coefficients of the relationship are derived through a relation with latitude using data from a range of values (see also Nikolov and Zeller (1992)). By now only the radiation on a horizontal surface at 274m elevation has been estimated and so a correction for elevation is needed. The corrections follows the exponential form of Beer's law and the radiation extinction coefficient is a function of solar radiation. Finally a correction is applied for tilted surfaces, which in our case is the earth's surface thus, slope and aspect were used.

Results were produced on a 1 km surfaces as mean monthly values of global incoming radiation. Validation of the output results of the model were compared with data from two meteorological stations (see Chapter 4).

5.2.2.4 Soil data

A large spatial soil database was obtained from the European Soil Bureau of the European Commission (Van Liedekerke *et al.*, 2006). The European Soil Database v2 ($10\text{km} \times 10\text{km}$) includes grids of many major soil parameters such as soil texture and soil depth, as a 10 km ESRI raster dataset. However, the dataset also contains a series of 1 km grids for the European continent, including soil texture, soil density, and organic carbon content in the topsoil (30cm). The database was initially constructed from a limited number of field measurements of organic carbon using a pedo-transfer concept to associate data with soil attributes such as texture and structure, land use, land cover and climatic criteria such as temperature. The newest version of the dataset was refined to a 1 km resolution using a revised pedo-transfer algorithm utilising an extended soil data set derived from the European Soil Database, combined with information about land cover, elevation and monthly temperature. The results were validated against real measurements for England, Wales and Italy. New datasets are being produced to provide a better validation set. Samples of organic carbon content were collected monthly between 1971 and 1990, whereas temperature data used were computed for the period 1980-1989. The resulting organic carbon content map for Europe thus, could be considered as the baseline of predictions in 1990 (Jones *et al.*, 2004).

From the European dataset, information about texture, density and organic carbon content were extracted for Scotland and georeferenced to the British national grid to match the climatic dataset. A surface of soil texture class for 3-PGN SPATIAL was created by redefining grid values from the empirical soil texture class surface. The surfaces for soil bulk density was created by redefined topsoil packing density classes. Values for bulk density for each class were derived from an extensive field survey of 45 Scots pine stands across Scotland (see Chapter 3). Carbon stocks of the topsoil (30 cm depth) were derived from the surface of organic carbon content by multiplying bulk density with depth of soil. The carbon stocks were then separated into labile and refractory pools based on estimated fractions for the two pools derived from literature (Wilson and Puri, 2001). Nitrogen stocks for labile and refractory pool at 30 cm depth were calculated from carbon stocks and the mean C:N ratios of the 45 sites.

5.2.3 Additional calculations

Annual net ecosystem production (P_E, $\mathrm{tC\ ha^{-1}\ yr^{-1}}$) was estimated as the difference between net primary production (P_N, $\mathrm{tC ha^{-1} yr^{-1}}$) and heterotrophic respiration (R_H, $\mathrm{tC ha^{-1} yr^{-1}}$). Annual heterotrophic respiration was estimated as the sum of soil fluxes of all soil carbon stocks (R_A =Y_l flux + Y_r flux + O flux).

$$P_E = P_N - R_H \tag{5.1}$$

Autotrophic respiration was estimated as a fixed proportion of P_G and P_N, while total ecosystem respiration was calculated as the sum of those two components (R_E = R_H + R_A, $\mathrm{tC\ ha^{-1}\ yr^{-1}}$), assuming that no other respiratory losses exist. Finally, ratios for belowground / total biomass and aboveground / total biomass were also estimated annually for the whole simulation period.

5.2.3.1 Spatial analyses and autocorrelation

All spatial analysis and calculations were performed using ArcInfo 9.0 workstation and desktop packages (Environmental Research Institute, Redlands, California, 2001). Measurements of spatial autocorrelation for the estimates of potential productivity and timber yields were produced to explore their spatial patterns. Spatial autocorrelation is the phenomenon where data are likely to have distances or length at which it is correlated with its self (O'Sullivan and Unwin, 2003). This autocorrelation results in the clustering of similar values in regions. To assess whether the produced outputs occurred in clusters, were independent or were dissimilar, the Moran's I statistic of spatial autocorrelation was determined for each variable and for each year between 1950 - 2050 from the 1 km grids and was averaged over the simulation period. Moran's I was estimated using Equation 5.2:

$$I = \frac{n}{\sum_{i=1}^{n}(y_i - \overline{y})^2} \frac{\sum_{i=1}^{n}\sum_{j=1}^{n} w_{ij}(y_i - \overline{y})(y_j - \overline{y})}{\sum_{i=1}^{n}\sum_{j=1}^{n} w_{ij}} \tag{5.2}$$

where y_i is the value of the attribute of the cell i, $\overline{y}$ is the overall mean value of the attribute, w_{ij} is the weight indicating whether the cell i and j are adjacent (1 if they are, otherwise 0) and n is the number of cells.

Moran's I is a measure similar to the non-spatial correlation statistic with the difference that it provides an estimation of the correlation of the attribute across space. Values could be either negative, zero or positive with negative values indicating that the spatial patterns of the measured variable appear to be very irregular (almost like a checkerboard), values close to zero indicating that spatial distributions are independent and random whereas positive values indicating that the attribute appears to be clustered and regionalised.

5.2.3.2 Correlation analysis

To determine which topographic or climatic variable have significant contribution to the existing patterns of potential productivity and yield, correlation analysis was performed between each variable of 3-PGN SPATIAL and latitude, elevation, slope, aspect and climatic variables. Due to the large number of possible climatic surfaces and the strong correlation amongst them a reduction was necessary.

Spatial principal component analysis (PC) was performed on all monthly surfaces of maximum and minimum temperature, precipitation, solar radiation and frost days separately. Spatial PC analysis works in a very similar way as with non spatial data. Eigenvalues and eigenvectors are estimated for each factor from a stack of spatial inputs surfaces, based either on a correlation or a covariance matrix. Factor surfaces with eigenvalues greater than one were used for further analysis.

Correlation coefficient (r_S) between the spatial distribution of a 3-PGN variable and the distribution of a topographic and climatic variable was then calculated between, for each year and averaged over the simulation period, based on Equation 5.3:

$$r_S = \frac{\sum_k^n (y_i - \overline{y_i}) \times (y_j - \overline{y_j})}{(\sqrt{\sum_k^n (y_i - \overline{y_i})^2} \times \sqrt{\sum_k^n (y_j - \overline{y_j})^2})} \tag{5.3}$$

where n is the total number of cells in a grid, i any cell on the first grid, j any cell on the second grid, y_i the value of the attribute of cell i, $\overline{y_i}$ the overall mean of the value of the attribute of the first grid, y_j the value of the attribute of cell j, $\overline{y_j}$ the overall mean of the value of the attribute of the second grid.

5.2.3.3 Regression Analysis

Further to correlation analysis, linear regression analysis was performed on a cell-by-cell basis for surfaces of net ecosystem production, accumulated net ecosystem production, mean annual increment, nitrogen availability, nitrogen uptake, autotrophic and heterotrophic respiration using surfaces from three different periods, that is 1975, 2000 and 2050 to identify which topographic or climatic variable is responsible for the observed spatial distribution.

Prior to analyses, dependent and independent variables were standardised between 0 and 1 (minimum and maximum values respectively) to eliminate differences in data range using Equation 5.4:

$$z = \frac{(y - y_{min}) \times (y'_{max} - y'_{min})}{y_{max} - y_{min}} \tag{5.4}$$

where y the value of the current grid cell, y_{min} and y_{max} the overall minimum and maximum value respectively for the untransformed grid and y'_{min} and y'_{max} the equivalent minimum and maximum values for the transformed grids. The new data range for all dependent and independent variables were transformed between 0 and 1 (maximum and minimum value respectively). Goodness of fit was assessed by the root mean square error and the chi-square between observed and predicted values, while the contribution of each independent variable to the spatial patterns of a dependent variable was given by the regression coefficients.

5.3 Results

5.3.1 Principal component analysis

Principal component analysis was performed separately for each set of monthly climatic variables (e.g., maximum temperature, minimum temperature, precipitation, solar radiation and frost days, see Figure 5.3). The logic behind this was to reduce the number of variables introduced in further analysis, but without loosing the information of the type of variable. Spatial principal component analysis was performed with

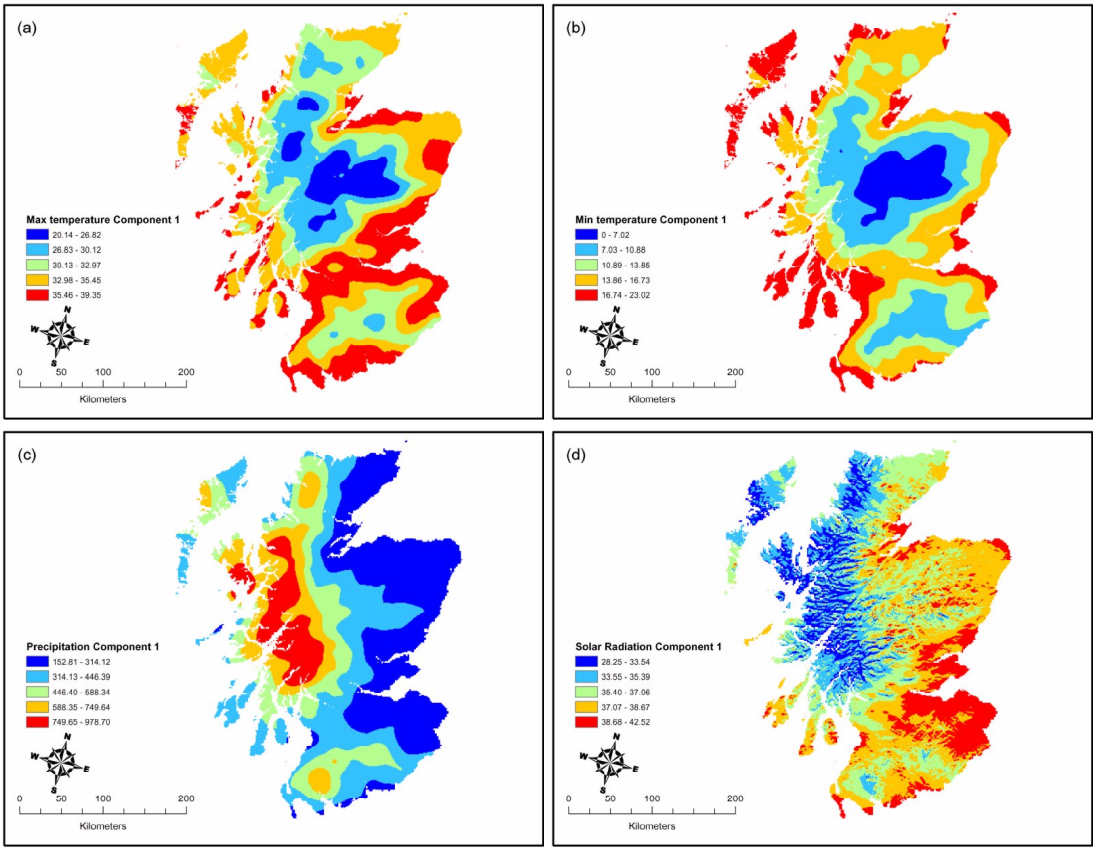

Figure 5.3: Principal component factor surfaces for winter (a) maximum temperature, (b) minimum temperature, (c) precipitation and (d) summer incoming solar radiation.

ArcInfo workstation. The analyses gave two major components for maximum temperature with eigenvalues greater than one, one component for minimum temperature, two components for frost days and one for solar radiation. However, the PCA for precipitation gave twelve components with eigenvalue above 1, which equals the number of initial variables included in the analysis, implying that all twelve monthly surfaces of

precipitation have a significant effect on the total variation for precipitation. However, to reduce the number of independent climatic variables only two components with the highest eigenvalues were used for further analysis.

The interpretation of all components was based on the values of the eigenvectors. The first component for maximum temperature (PC_{Tmax_1}) was positively affected by maximum temperature values of the winter months (more specifically from November to February), thus it was characterised as winter maximum temperature. The second major component on the other hand (PC_{Tmax_2}) was positively effected by maximum temperatures during the summer months (more specifically June, July and August), while it was a negatively affect from the winter months, thus it was characterised as summer maximum temperatures. On the other hand, eigenvectors for minimum temperature (PC_{Tmin_1}) indicated that the single major component was mainly explained by minimum temperature of January and February. The first component of frost days (PC_{FD_1}) was mainly effected by values for the months between November to March and so it is characterised as winter frost days, while the second component was mainly effected negatively by values for the same season and so it was characterised as lack of winter frost days. Frost days during the summer period had little effect on the second component for frost days (PC_{FD_2}). The single factor produced in the PCA for solar radiation (PC_{SolRad_1}) was mainly explained by values for June, July and August and so it was characterised as summer incoming solar radiation. Interpretation of the precipitation factors on the other hand was not so easy. Nevertheless, the variance of the first component factor (PC_{Precip_1}) was mainly explained by precipitation values for the winter months (especially for the period between October through March), thus it was characterised as winter precipitation, while the second component factor's (PC_{Precip_2}) variance was mainly explained by values of July, August and September precipitation and so it was characterised as autumn precipitation.

5.3.2 Autocorrelation analysis

Figure 5.4 gives the average Moran's I autocorrelation index over the simulation period for 27 of the major outputs of 3-PGN SPATIAL. Only positive autocorrelations were

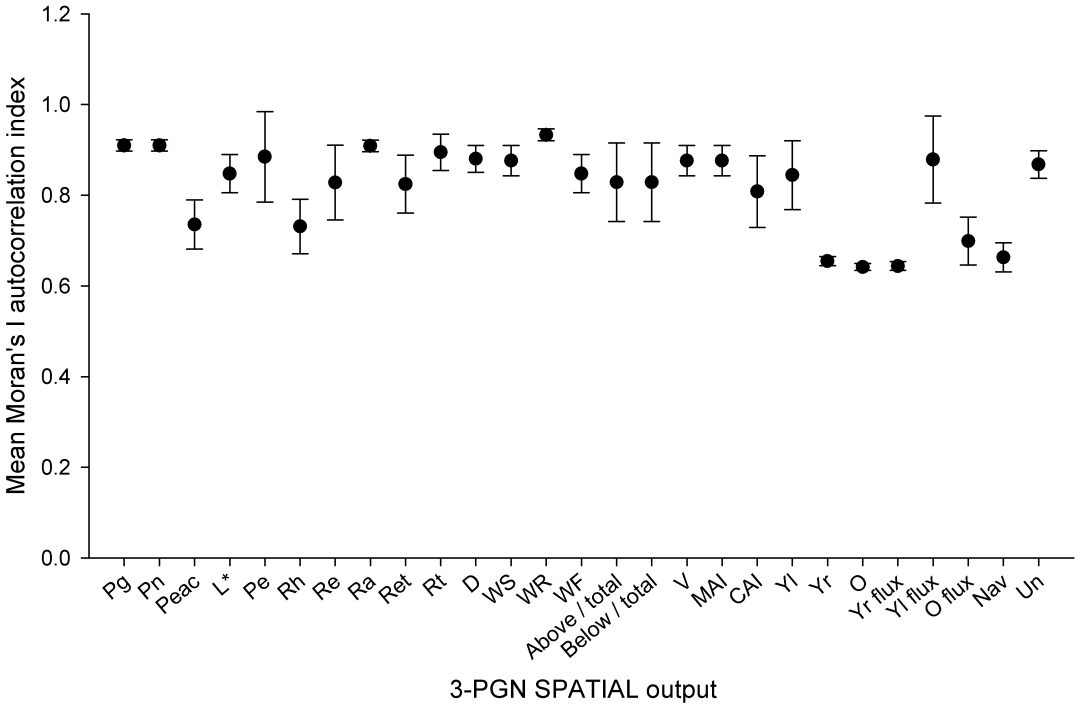

Figure 5.4: Mean Moran's I autocorrelation coefficient (unitless) for 100 years simulation period, for 27 major outputs of 3-PGN SPATIAL. All outputs of 3-PGN SPATIAL showed strong positive autocorrelation which indicates a regionalisation of spatial patterns. A slightly stronger clustering effect was shown by root biomass whereas the old carbon pools had the most spatially randomised patterns. Bars illustrate standard deviation from the mean, which indicate the temporal variability of spatial autocorrelation. Spatial patterns of old carbon pool did not change significantly, while on the other hand spatial patterns of net ecosystem production varied the most through out the simulation period.

observed, which indicated that spatial patterns were not random. Coefficients varied between +0.64 and +0.93 with the majority of outputs having values close to +0.8. Root biomass showed the most regionalised spatial patterns, while the old organic carbon pool the less regionalised patterns. Heterotrophic respiration, and specifically the fluxes from the labile litter decomposition pool, also appeared to have significantly less clustered spatial patterns. The bars of the standard deviation from the mean indicated the temporal variability of the autocorrelation of a certain variable. Spatial patterns of net ecosystem productivity changed significantly throughout the simulation period, while time did not appear to have much affect on the patterns of the old carbon pool. Ecosystem respiration patterns (especially the heterotrophic component) changed significantly through time (Figure 5.5). The components of heterotrophic respiration resulting to temporal changes in spatial patterns were the carbon fluxes from the labile, fast decomposed litter and from the old carbon component. Both of these

processes contribute to changes in net ecosystem productivity from a randomised to a more clustered distribution after the first fifteen years of the simulation period. Interestingly, after 90 years when respiration started to exceed productivity, patterns of net ecosystem production started to become more randomised (Figure 5.5).

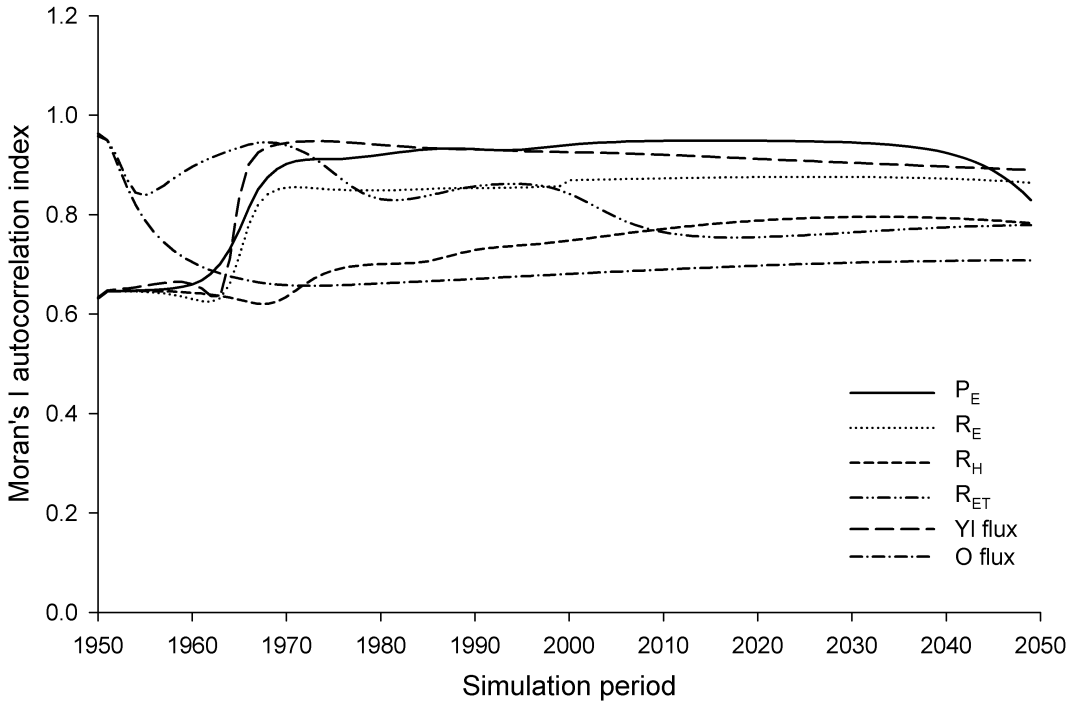

Figure 5.5: Temporal changes of Moran's I autocorrelation index for net ecosystem productivity ($P_{E_{AC}}$, $\mathrm{tC\ ha^{-1}\ yr^{-1}}$), ecosystem respiration (R_E, $\mathrm{tC\ ha^{-1}\ yr^{-1}}$), heterotrophic respiration (R_H, $\mathrm{tC\ ha^{-1}\ yr^{-1}}$), annual evapotranspiration (R_T, mm), outfluxes for young and labile soil carbon pool (Y_l flux, $\mathrm{tC\,ha^{-1}\,yr^{-1}}$) and outfluxes for old soil carbon pool (O flux, $\mathrm{tC\,ha^{-1}\,yr^{-1}}$). Positive autocorrelation indicate clustered spatial patterns. Old carbon pool and evapotranspiration patterns start with a very clustered pattern, whereas the opposite occurs for the other variables. Autocorrelation index is low for net ecosystem productivity for the first 12 - 15 years, then regionalisation occurs until the age of 90 where again randomization of the spatial patterns is taking place.

5.3.3 Correlation analysis

The results of the correlation analyses performed on 26 of the major outputs of 3-PGN SPATIAL are presented in Figures 5.6, 5.7, 5.8 and 5.9. The correlation coefficients were estimated for each simulation year and then averaged throughout the period. Bars represent the standard deviation over time, from the mean (significant at $P < 0.01$, $n = 157,500$). The value of correlation coefficients with topographic variables such as

latitude, elevation and slope did not exceed 0.54 (Figure 5.6a, b and c). More specifically, annual transpiration correlated negatively with latitude ($r_S = -0.43$), while old carbon pool was positively related with latitude with $r_S = 0.26$. The majority of 3-PGN SPATIAL outputs was positively correlated with latitude except $P_{E_{AC}}$, P_E, W_R, R_{ET}, R_T, and belowground / total biomass.

On the other hand, the majority of 3-PGN SPATIAL outputs are negatively correlated with elevation except the flux from Y_r, the pools of Y_r, O and N_{AV}. The same four outputs appeared to be positively correlated with slope. Net ecosystem productivity had the largest negative correlation with elevation ($r_S = -0.54$), while the young refractory carbon pool appeared to have the largest positive correlation with $r_S = 0.34$. Root biomass appeared to be strongly correlated with slope ($r_S = -0.45$) while aboveground / total biomass ratio the output more strongly correlated with slope. High standard deviation for Y_l flux and N_{AV} suggests that correlation changes throughout the simulation period. A better look at the time patterns of the correlation coefficient of N_{AV}, showed that nitrogen availability was negatively correlated with elevation for the first twenty years after stand establishment and then it became positively correlated.

Correlation with climatic variables was conducted using the reduced variables produced by the principal component analyses. Figure 5.7 illustrates the results of the correlation analysis with the first two major components of maximum temperature (Figure 5.7a and b) and the first component of minimum temperature (Figure 5.7c). The majority of 3-PGN SPATIAL outputs were positively correlated with winter maximum and minimum temperatures, while they are negatively correlated with summer maximum temperatures. However, maximum temperatures during the winter months appeared to have a negative effect on soil carbon stocks and nitrogen availability. Moreover, transpiration and evapotranspiration losses were significantly related with summer maximum temperatures. Interestingly, below / total biomass was also slightly related to maximum summer temperatures. Finally, winter minimum temperature appeared to have a highly significant effect for the majority of the outputs. Again, soil carbon is negatively related to winter minimum temperatures although not very strongly, together with nitrogen availability and aboveground / total biomass ratio. The highest positive

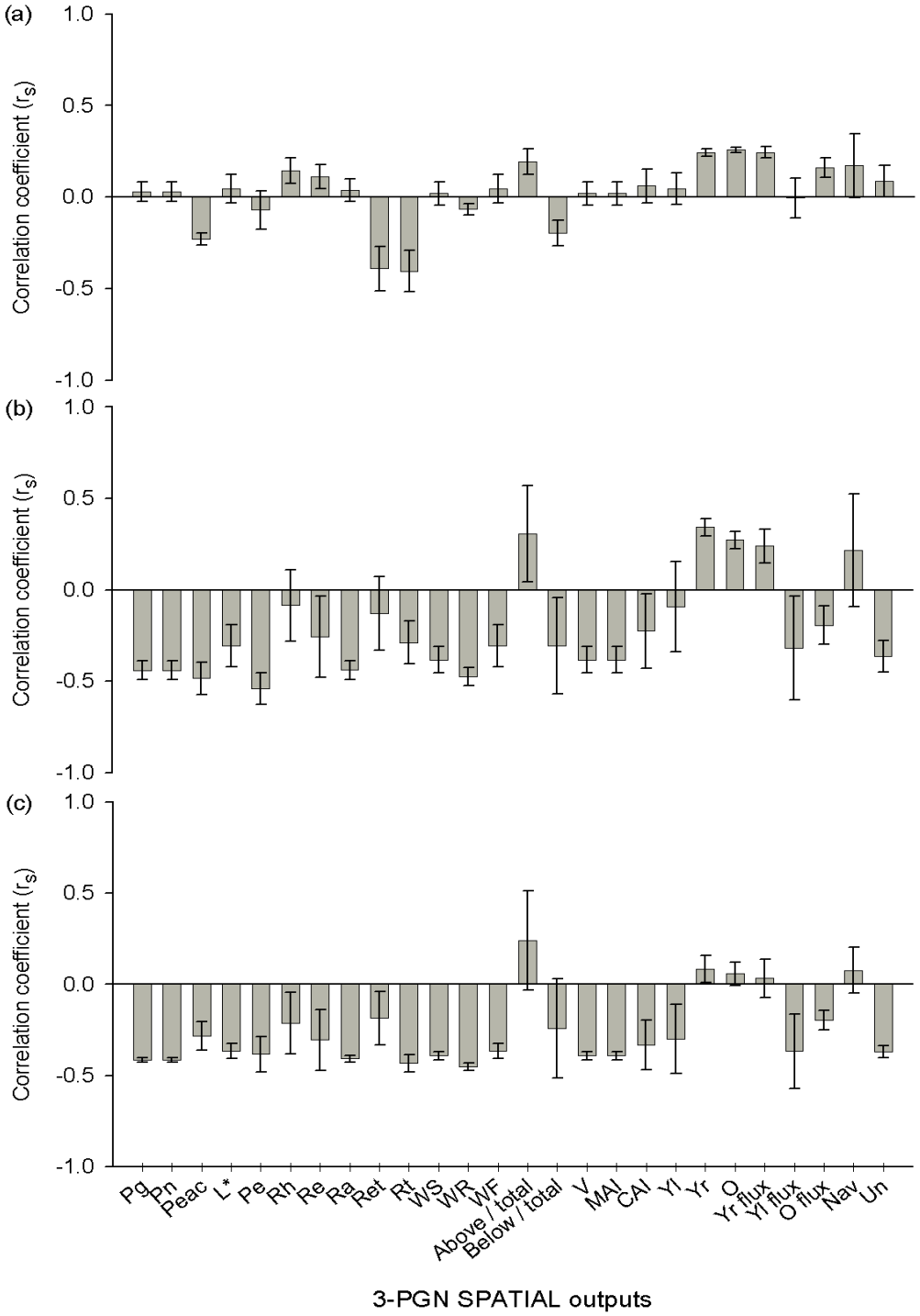

Figure 5.6: Mean correlation coefficient for 26 major outputs of 3-PGN SPATIAL over the simulation period with (a) latitude (decimal degrees), (b) elevation (m) and (c) slope (degrees). Bars indicate standard deviation from the mean.

correlation with winter maximum temperature appeared to be with root biomass, while the highest negative correlation was with above / total biomass ratio. Summer maximum temperatures had the highest positive correlation with transpiration, while carbon

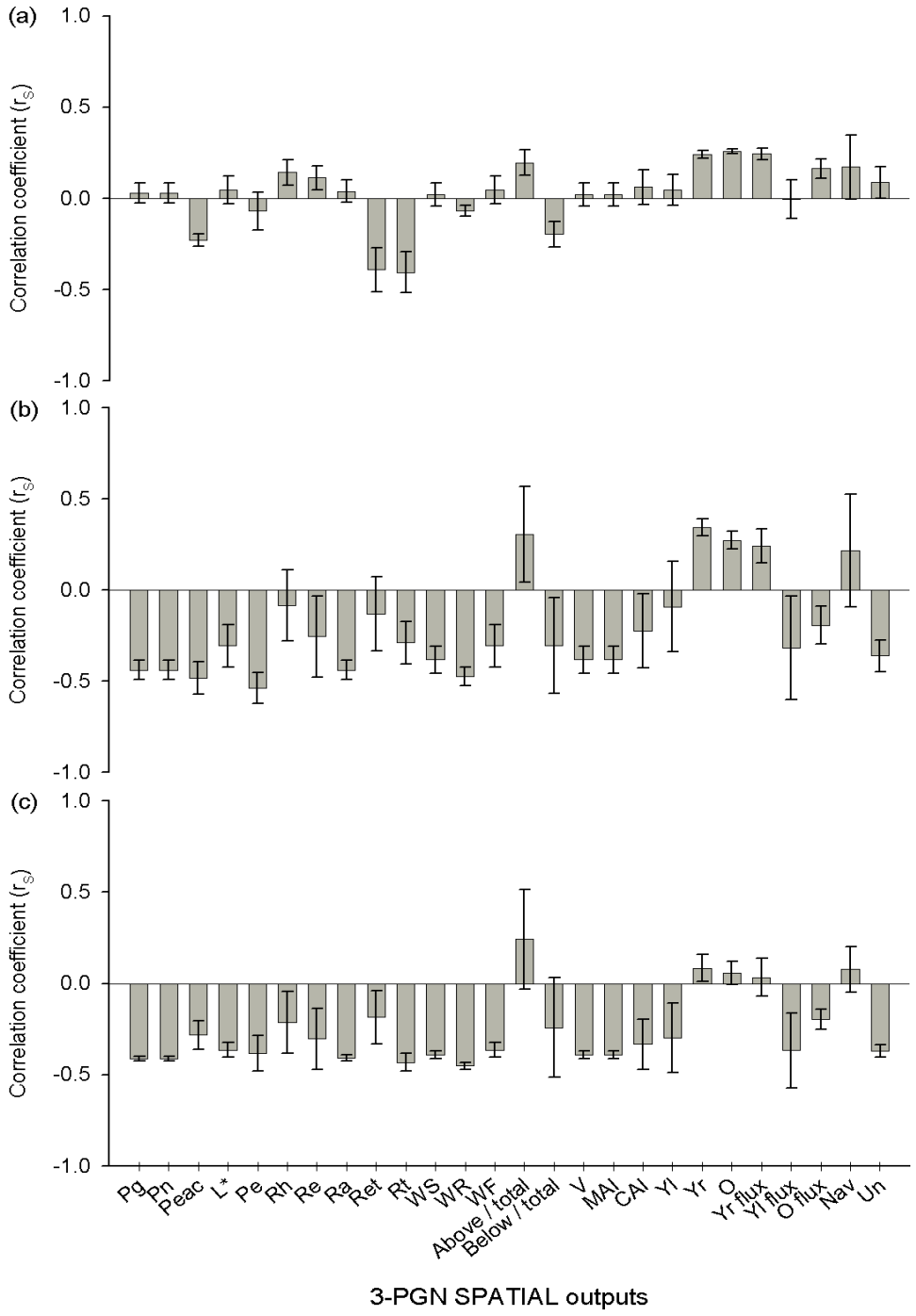

Figure 5.7: Mean correlation coefficient for 26 major outputs of 3-PGN SPATIAL over the simulation period with (a) winter maximum temperature (PC_{Tmax_1}), (b) summer maximum temperature (PC_{Tmax_2}) and (c) winter minimum temperature (PC_{Tmin_1}). Bars indicate standard deviation from the mean.

fluxes from the old carbon pool had the highest negative correlation.

From Figure 5.8 it is clear that summer precipitation did not correlate significantly with

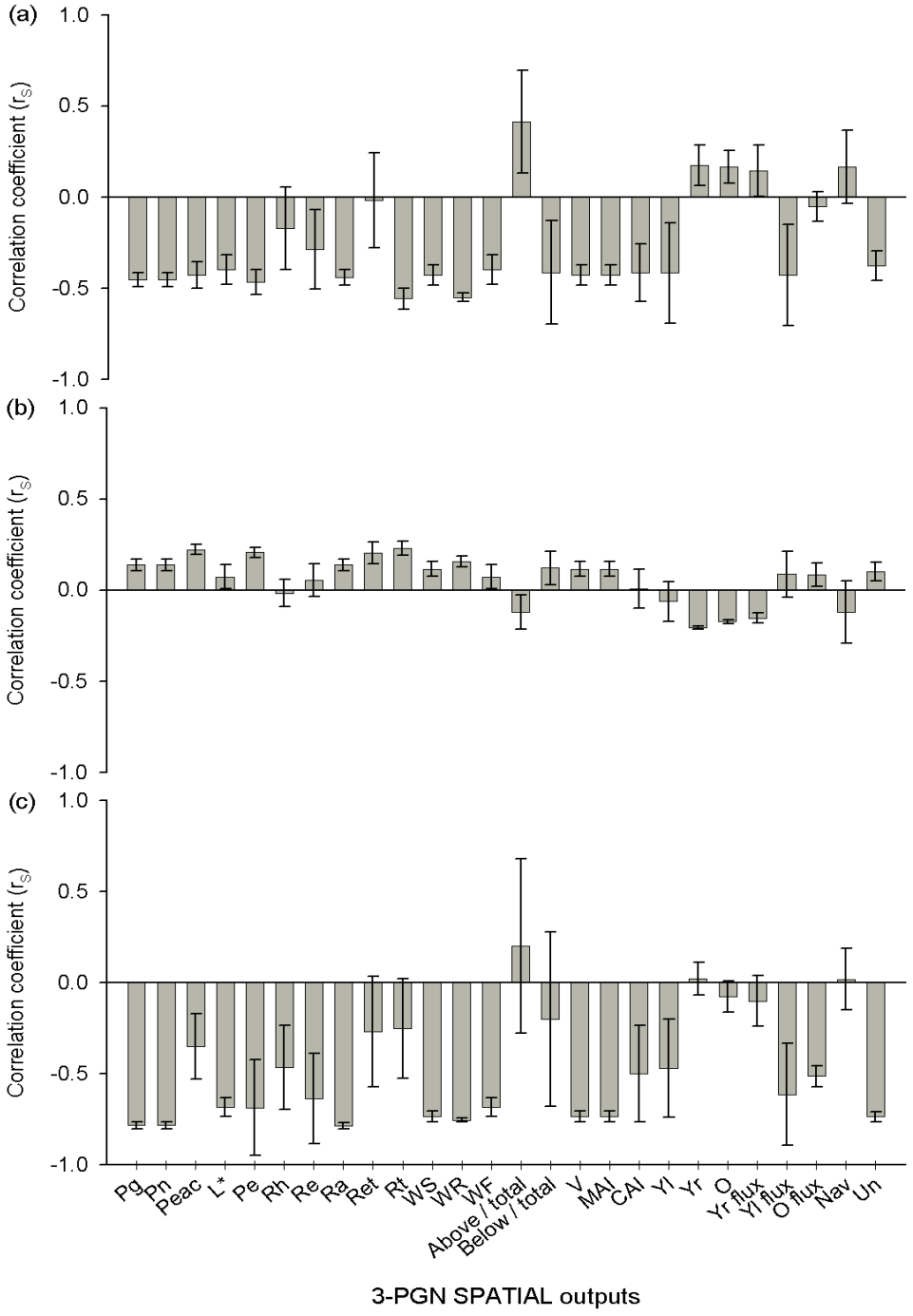

Figure 5.8: Mean correlation coefficient for 26 major outputs of 3-PGN SPATIAL over the simulation period with (a) winter precipitation (PC_{Precip_1}), (b) summer precipitation (PC_{Precip_2}) and (c) winter frost days (PC_{FD_1}). Bars indicate standard deviation from the mean.

almost any single 3-PGN SPATIAL output. However, there was a negative correlation with all soil carbon pools and with nitrogen availability. On the other hand, winter precipitation appeared to result in conclusions of the opposite sign and with higher

values compared to summer precipitation. Correlation was negative for all the outputs except carbon pools and nitrogen availability. Transpiration had the strongest negative correlation with winter precipitation ($r_S = -0.56$), while aboveground / total biomass ratio had the highest positive correlation ($r_S = 0.41$). Young refractory carbon pool had the highest negative correlation with summer precipitation ($r_S = -0.21$) whereas annual evapotranspiration had the highest positive correlation ($r_S = 0.23$). Winter frost days appeared to have highly significant negative effects on autotrophic respiration, with $r_S = -0.79$. Finally, summer frost days (Figure 5.9) did not appear to have strong effect on any of the outputs, except on soil carbon pools, with $r_S = 0.29$ for young refractory and $r_S = -0.56$ for the old carbon pool, while it had a negative correlation with annual evapotranspiration ($r_S = -0.37$). Moreover, summer incoming solar radiation was significantly related to carbon and timber, production or loss. The greatest correlation was with annual transpiration while soil carbon pools appeared to have again a non-significant negative correlation with solar radiation.

The most significant topographic and climatic variables that affected ecosystem carbon accumulation and timber production are reported in Figure 5.10. Winter maximum temperatures had the most significant effect on carbon accumulation ($P_{E_{AC}}$, $r_S = 0.61$), while winter minimum temperatures ($r_S = 0.48$) and incoming solar radiation ($r_S = 0.41$) contributed also significantly too. Moreover, as altitude increased, carbon accumulation potentials decreased. Winter precipitation also significantly restrict carbon accumulation.

On the other hand, timber production expressed as mean annual volume increment (Figure 5.10) was highly significantly correlated with winter minimum temperatures ($r_S = 0.71$), while winter maximum temperatures was also associated significantly with timber production ($r_S = 0.60$). However, the effect of altitude was not so clearly defined. Nevertheless, winter frost days appeared to have a significant restricting effect on timber growth ($r_S = -0.73$) with winter precipitation also significantly and negatively related to mean annual volume increment($r_S = -0.43$).

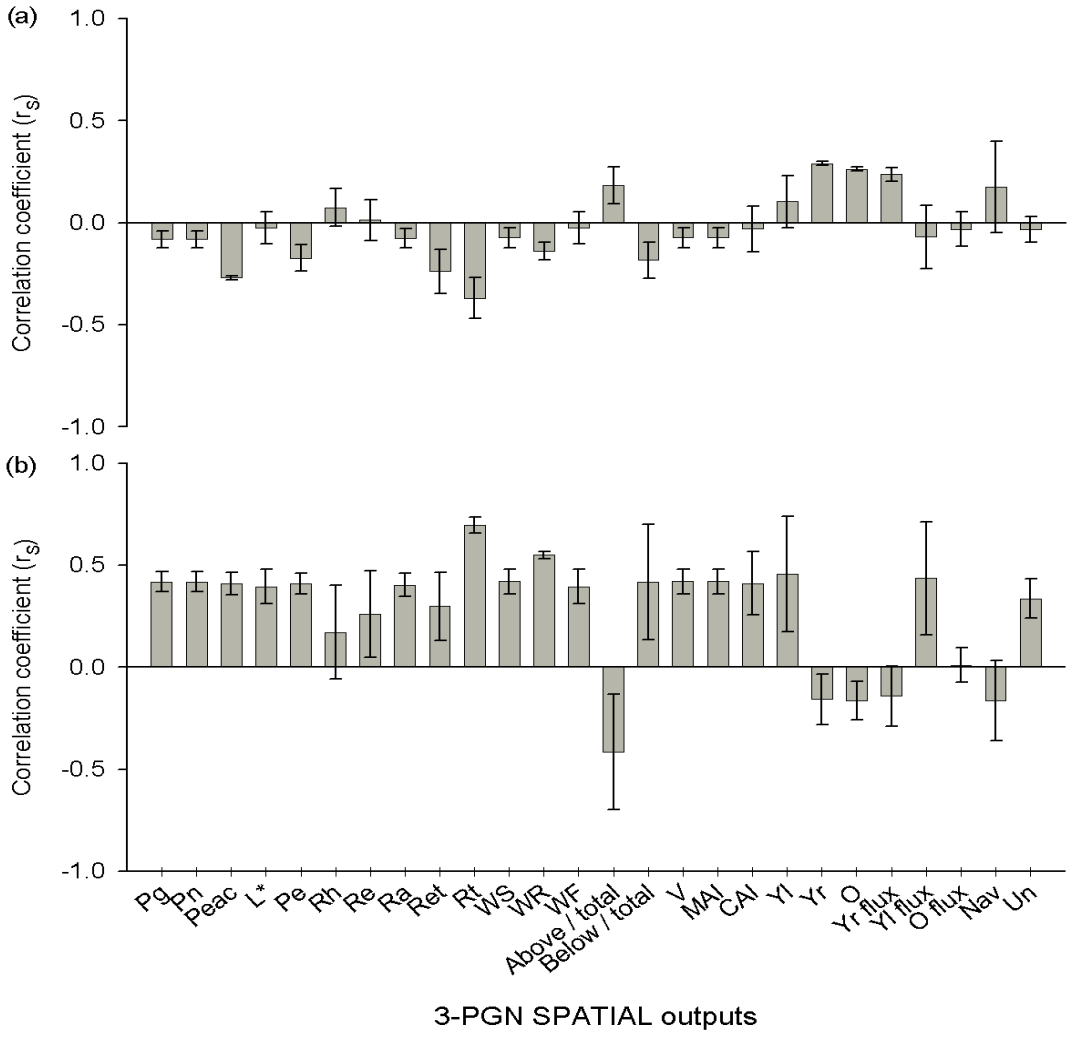

Figure 5.9: Mean correlation coefficient for 26 major outputs of 3-PGN SPATIAL over the simulation period with (a) summer frost days (PC_{FD_2}) and (b) summer incoming solar radiation (PC_{SolRad_1}). Bars indicate standard deviation from the mean.

5.3.4 Regression analysis

The most significant results of the regression analysis are presented in Table 5.1. The results support the findings from the correlation analysis that winter minimum temperature and maximum temperatures are the most significant climatic variables which contribute more to the current patterns of productivity and timber production. The results also showed that spatial patterns of mean annual increment at the early stages of the simulation (i.e., 1975) matched those of winter maximum and minimum temperature (i.e., $MAI_{\ 1975}$, Table 5.1). However, as time progressed, other factors affected timber

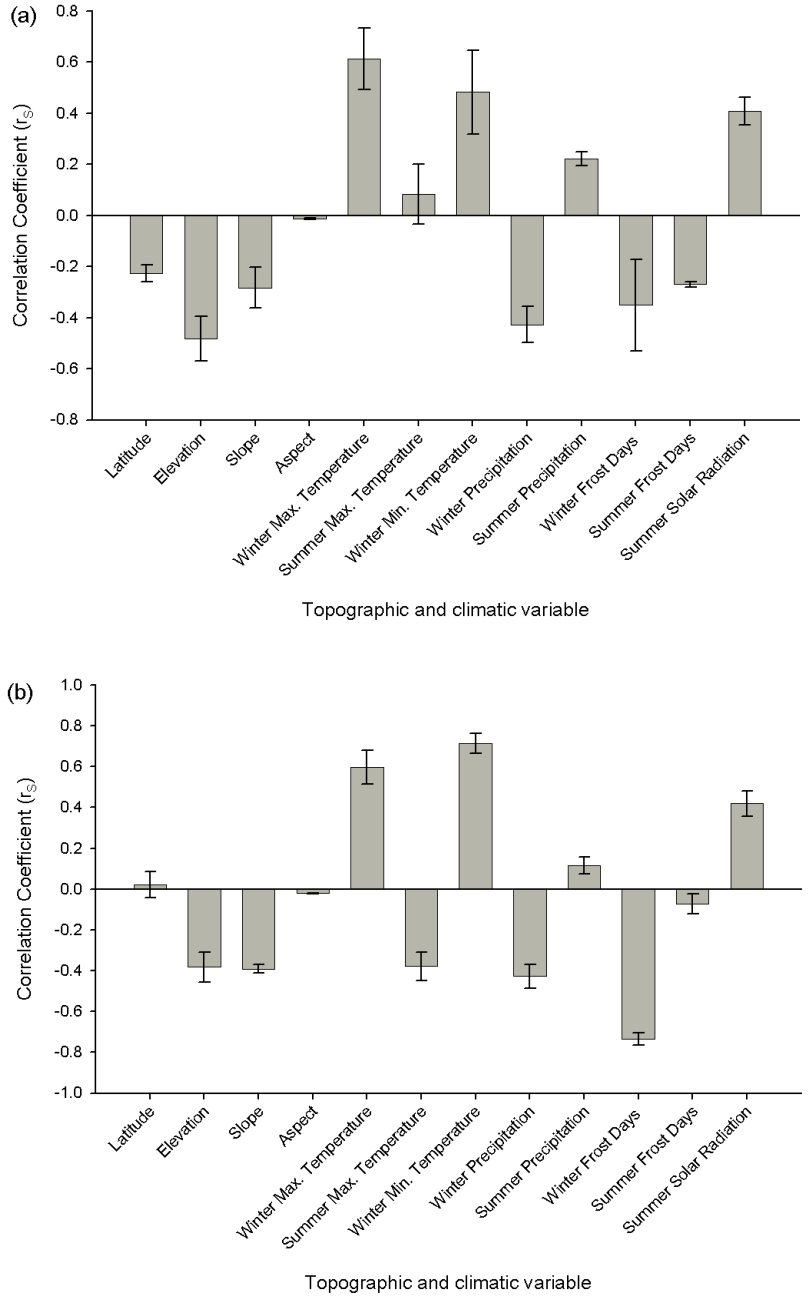

Figure 5.10: Correlation coefficients with a range of topographic and climatic variables for (a) accumulated net ecosystem production ($P_{E_{AC}}$ $\mathrm{tC\ ha^{-1}}$) and (b) for mean annual increment (MAI $\mathrm{m^3\ ha^{-1}\ yr^{-1}}$). Bars indicated standard deviation of the mean over the 100 years of simulation period. Carbon accumulation of a Scots pine ecosystem is mostly affected by maximum air, temperature while minimum temperatures and solar radiation have a significant effect. It is also clear that carbon accumulation is less for higher altitude regions of Scotland. On the other hand, timber production is mainly effected by minimum air temperature, while again maximum temperatures and solar radiation have a significant effect. Interesting is the negative correlation with precipitation suggesting that wetter sites do not accumulate more carbon or produce more timber.

Table 5.1: A summary of the results of spatial regression analysis between carbon and water fluxes as well as timber production with climatic and topographic variables. Standardised values of dependent and independent variables were used to fit grid data surfaces to a linear model $y = a + bx$ where a is the intercept and b the slope of the relation. The linear model was used to identify the factor having a greater contribution to the spatial patterns of carbon and yield production and fluxes. A relationship close to 1:1 suggests that spatial patterns between dependent and independent variable match. Results shown that maximum and minimum temperature were the two major inputs whose spatial patterns match those of fluxes. In particular, the relationship between annual transpiration ($R_{T\ 1975}$, mm) and mean annual increment ($MAI_{\ 1975}$, $\mathrm{m^3\ ha^{-1}\ yr^{-1}}$) in the year 1975 has similar patterns with maximum temperature component factor 1 (PC_{Tmax_1}, see also Figure 5.11).

	Dependent	Independent	a	b	RMSE	χ^2
Intercept < 0.2 slope > 0.5	$MAI_{\ 1975}$	PC_{Tmax_1}	0.02	0.52	0.09	611.40
	$MAI_{\ 1975}$	PC_{Tmin_1}	-0.02	0.66	0.07	366.93
	$R_{T\ 1975}$	PC_{Tmax_1}	0.16	0.77	0.09	621.19
	$R_{A\ 1975}$	PC_{Tmax_1}	0.10	0.52	0.10	699.70
	$R_{A\ 1975}$	PC_{Tmin_1}	0.05	0.69	0.07	389.55
	$R_{A\ 2000}$	PC_{Tmin_1}	0.07	0.57	0.08	412.45
	$R_{A\ 2050}$	PC_{Tmin_1}	0.02	0.57	0.08	504.73
Intercept < 0.2 $0.3 <$ slope < 0.5	$MAI_{\ 2050}$	PC_{Tmax_1}	0.17	0.32	0.10	685.21
	$MAI_{\ 2000}$	PC_{Tmin_1}	0.16	0.48	0.07	379.38
	$MAI_{\ 2050}$	PC_{Tmin_1}	0.11	0.47	0.08	488.53
	$R_{T\ 2050}$	PC_{Tmax_1}	0.15	0.47	0.10	649.30
	$R_{H\ 2050}$	PC_{Tmin_1}	0.15	0.35	0.09	541.48
	$R_{A\ 2000}$	PC_{Tmax_1}	0.13	0.39	0.10	697.93
	$R_{A\ 2050}$	PC_{Tmax_1}	0.07	0.41	0.10	768.15

production and resulted in a differentiation of the patterns relative to the responding potentials for temperature. This suggests that temperature was likely the most significant factor affecting patterns of growth in the early stages of a stand's establishment comparing the slopes of the responses for MAI in Figure 5.11.

Spatial patterns of autotrophic respiration were also associated with the patterns of maximum winter temperature at the beginning of a stand establishment, while minimum winter temperature patterns contributed more to the spatial patterns later on (Table 5.1). Similar results were obtained for net primary production. Finally, spatial patterns of transpiration were effected by winter maximum temperature throughout stand development (Table 5.1), however this relation becomes weaken with age as other climatic parameters become more important.

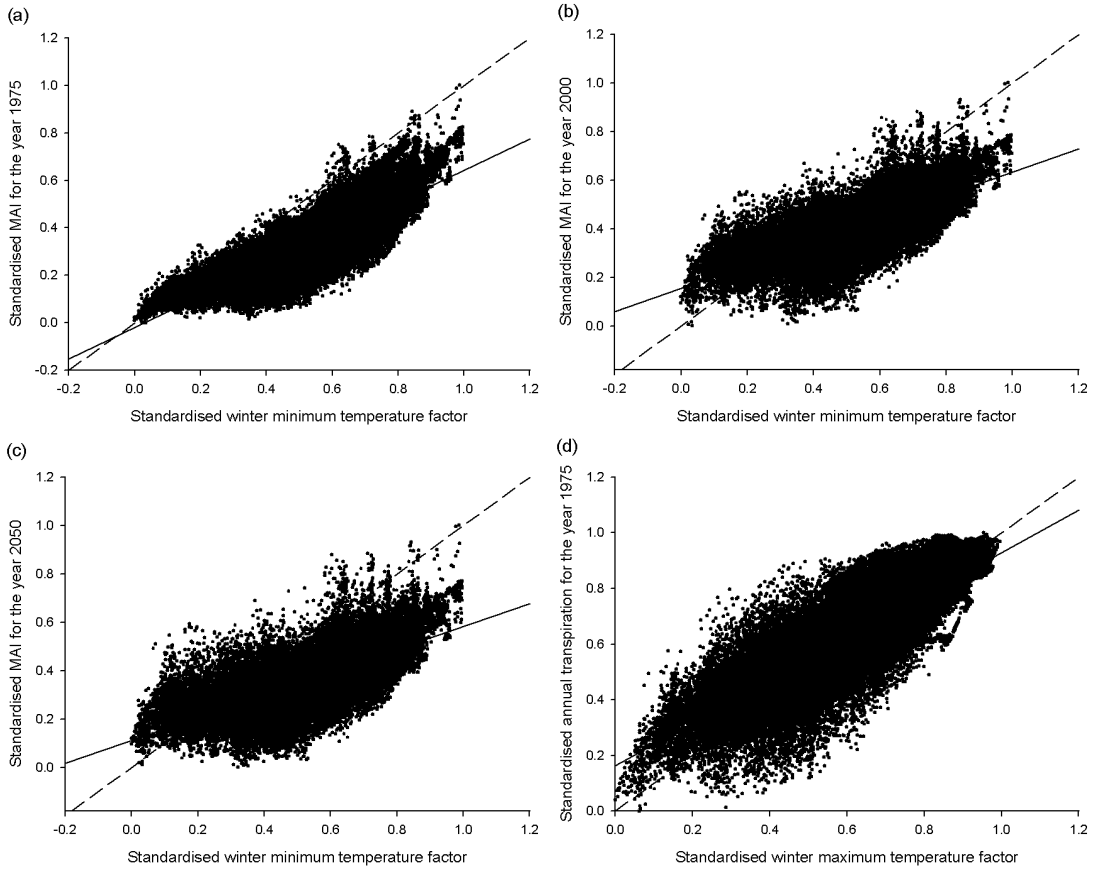

Figure 5.11: Relationship between standardised component factor of minimum winter temperature with standardised mean annual increment (MAI, $\mathrm{m^3\ ha^{-1}\ yr^{-1}}$) (a) for the year 1975, (b) for the year 2000 and standardised annual transpiration (R_T, mm) (c) for the year 1975 and (d) for the year 2000. Dashed line indicate the 1:1 relationship.

5.3.5 Timber and carbon predictions and spatial distribution

Figures A.1, A.2, A.3, A.4, and A.5 show the predicted spatial patterns of net ecosystem production, net primary production, ecosystem respiration, standing volume and mean annual increment respectively, for Scots pine across Scotland at the age of 25, 50, 75 and 100 (Pages 280, 282, 284, 286, 288 of Appendix A).

Net ecosystem production (Figure A.1) ranged between 2.46 - 2.76 $\mathrm{tC\ ha^{-1}\ yr^{-1}}$ after 25 years, while the majority of the regions have ecosystem production between 1.6 - 1.92 $\mathrm{tC ha^{-1} yr^{-1}}$. Interesting is the existence of small regions, mainly at the east coast of Scotland with P_E between 2.21 - 2.48 $\mathrm{tC\ ha^{-1}\ yr^{-1}}$.

3-PGN SPATIAL predicted P_N 25 years after establishment, between 1.26 $\mathrm{tC ha^{-1} yr^{-1}}$

for the highest mountain regions to 5.68 $\mathrm{tC\,ha^{-1}\,yr^{-1}}$ for the north-west and north-east coastal regions (Figure A.2). The majority of the most productive regions of Scotland 25 years later include the central and the north-east coastal line, having a production between 2.92 - 3.46 $\mathrm{tC\ ha^{-1}\ yr^{-1}}$. As time progressed, production dropped between 0.14 and 0.69 $\mathrm{tC\ ha^{-1}\ yr^{-1}}$ but with south-east coast still being very productive with P_N between 0.7 - 1.25 $\mathrm{tC\ ha^{-1}\ yr^{-1}}$.

Mean annual increment (Figure A.5) ranged from 3 $\mathrm{m^3\ ha^{-1}\ yr^{-1}}$ for the inner region of Scotland including mountain regions to 9 $\mathrm{m^3\ ha^{-1}\ yr^{-1}}$ for southern coastal regions with an average of 6.9 $\mathrm{m^3\ ha^{-1}\ yr^{-1}}$ (± 0.974). Stand volume on the other hand (Figure A.4), reached values between 649 and 754 $\mathrm{m^3\ ha^{-1}}$.

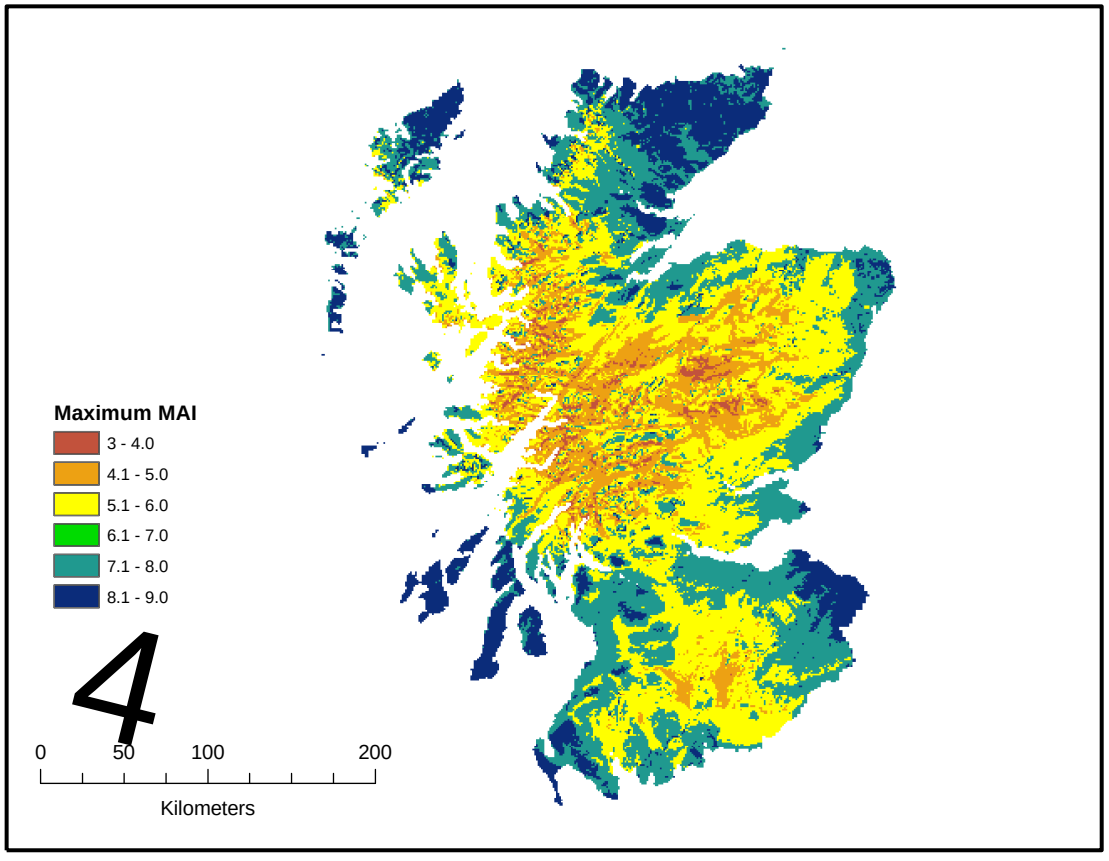

Figure 5.12: Potential maximum MAI ($\mathrm{m^3\ ha^{-1}\ yr^{-1}}$) as it was predicted by 3-PGN SPATIAL. Results shown clearly four major zones of potential timber increment with the highest timber production near the east, north-east and south-west coast line. Moving inland, potential timber production is reduced until reaching the west exposed mountain regions of Ben Nevis and the east-central region of Cairngorm mountains. Also it is clear that the patterns match those of precipitation, sunshine (Figure 5.1) and elevation (Figure 5.2), which suggests that western regions of Scotland with high precipitation and low sunshine are not suitable for Scots pine growth as potential growth is very low.

Figure 5.12 (page 171) illustrates the predicted maximum MAI for Scots pine across Scotland. Four zones could be distinguished with the highest productivity closer to the coastal line of east, north-east and south west, while the mountain regions of Cairngorms and Ben Nevis appear the least productive. Interesting is that the model predicted low production for the native woodlands of Glen Affric and Glen Coe (around 4 - 5 $\mathrm{m}^3\ \mathrm{ha}^{-1}\ \mathrm{yr}^{-1}$).

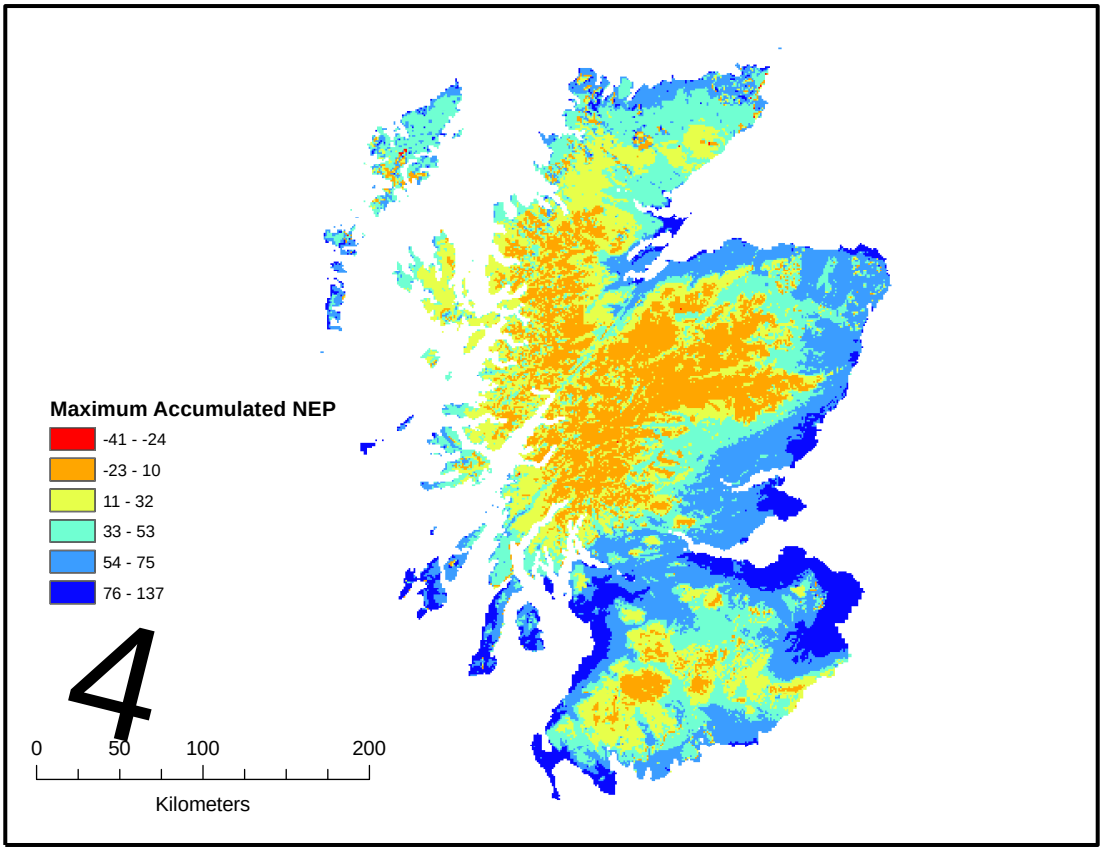

Figure 5.13: Maximum ecosystem carbon accumulation ($P_{E_{AC}}$, $\mathrm{tC\,ha}^{-1}$) as it was predicted by 3-PGN SPATIAL. Carbon storage appears to have similar zonation as potential timber production. East-west patterns exist with the eastern coastal line more productive in terms of carbon. Interesting is the north-eastern region, which appears to be quite sheltered from atlantic winds and rainfall (Figure 5.1) resulting into greater carbon accumulation. Mountain regions of Cairngorms on the east, and Ben Nevis on the west, appeared to have negative values indicating sites not suitable for Scots pine growth.

On the other hand, Figure 5.13 (page 172) shows the predicted spatial patterns of accumulated net ecosystem production. Again coastal line of the east appeared to accumulated greater amount of carbon (approximately 137 $\mathrm{tC\ ha}^{-1}$). Result also showed a large region of central highland region including the mountainous regions of Ben Nevis and Cairngorm having negative values, indicating carbon loss.

5.4 Discussion

5.4.1 Identifying climatic and topographic effect on growth

Correlation analysis showed that the majority of 3-PGN SPATIAL outputs were not correlated with latitude except annual evapotranspiration and annual transpiration ($r_S = -0.39$ and $r_S = -0.40$ respectively). A negative correlation (Figure 5.6) indicated that southern stands of Scots pine transpired more water than northern once. Differences in incoming solar radiation between north and south are not as extreme as it is between South-East and North-West (Figure 5.6), nevertheless, they created differences in temperatures causing differences in vapour pressure deficit. Higher maximum and minimum temperatures (Figure 5.6) in the South resulted in higher VPD leading to stomatal opening and losses of water. The central lowland region between Glasgow and Edinburgh, appeared to have the highest values of temperature throughout the year. Together with the south east coast they are expected to have the greatest water loss through evapotranspiration. Young refractory and old carbon pools also appeared positively correlated with latitude. Northern stands had more soil carbon stored in the soils either as slowly decomposed organic carbon or as humified and even slowly decomposed carbon. This comes in agreement with field observations of soil texture (Chapter 3). Southern stands and more specifically those in low elevation are based on freely drained, with low water potentials and possibly with low nutrient availability. The low nutritional status of the southern stands has slightly appeared in our analysis as a weak correlation between nitrogen availability and latitude (Figure 5.6).

Elevation on the other hand, appeared to be significantly correlated with the majority of outputs. High altitude stands have less autotrophic and heterotrophic respiration due to lower production. Foliage biomass and consequently L^*, is also less for high altitude as the driving factor for foliage expansion, solar radiation, is limited (Figure 5.1). Evapotranspiration is less effected by elevation in comparison to transpiration, suggesting that evaporation is not affected greatly by elevation. Grant (2004) showed that evapotranspiration rates are reduced when soil water is in excess. Although high altitude sites have greater slopes, high density soils help retain water, while consistent

and evenly distributed precipitation throughout the year keep air and soil humidity levels very high, reducing evapotranspiration. However, temperature difference are more likely to explain such a elevational effect.

The ratio between above and total biomass is positively correlated with altitude showing a higher allocation to aboveground biomass. This could be due to the fact that most soil types at low elevation sites are freely drained and possibly with low nutrient status, which drives trees to allocate more for a sufficient root system development. Moreover, high altitude sites are exposed to strong winds enhancing aboveground allocation for mechanical support against wind forces, which is also supported by the negative correlation of root biomass and elevation. Also, volume stocks and yield increments were lower for higher elevation, as a result of lower photosynthetic capacity.

Examining the correlation of soil carbon fluxes with elevation, young labile carbon pool appeared negatively affected by altitude. Stands in high elevation do not produce enough leaf biomass to support a constant input of litter into the soil. A limited input of litter into the fast decomposed soil carbon pool will result in lower carbon stocks and lower soil respiration. Differences in soil types also may have contributed to differences in decomposition. On the other hand, lower soil temperature will significantly slow decomposition. In 3-PGN SPATIAL, decomposition is directly affect by air temperature using the assumption that most of the decomposition takes place close to the surface and thus soil temperatures are similar. This big assumption certainly adds a bias into model's estimations. Nevertheless, basic concepts are captured correctly and such bias can be removed by further developing the model with the introduction of a soil temperature estimation based on air temperature and basic soil attributes (e.g., texture). Young refractory and old carbon pools on the other hand, were positively correlated with elevation, suggesting either a reinforced humification process with altitude or low soil respiration. For high humification rates, high decomposition rates are necessary. However, the correlation of Y_r respiration with elevation showed that low air temperature will cause less decomposition and so lower respiration rates. The low significant effect of air temperature to respiration of refractory soil carbon is also illustrated by Figure 5.7 with r_S equal to -0.25, -0.31 and 0.14 respectively for win-

ter maximum, summer maximum and winter minimum air temperature. Thus a safe conclusion is that the increase is due to lower respiration (O flux in Figure 5.6).

The lower productivity with elevation is also supported by the fact that nitrogen uptake is lower when Scots pine is growing in high altitude sites. Nitrogen availability is higher for high altitude sites due to faster decomposition of young labile carbon, while it is known that labile microbial activity is the most significant factor for soil nitrogen availability (Chapter 4). Nitrogen uptake on the other hand, was shown to be significantly reduced with elevation as there is a smaller photosynthetic activity due to low incoming solar radiation and less leaf development causing a smaller nitrogen demand. Additionally, low air temperature will restrain growth by stopping photosynthesis, limiting again the demand for nitrogen. Considering that the fertility rating is the ratio between nitrogen availability and nitrogen uptake, high elevation sites will have high fertility ratings. This however, does not mean that site is suitable for Scots pine growth as FR is no more a site classification variable, but an internal fertility status indicator. In this occasion, the model suggests that potentially these sites have the nutritional capability of establishing Scots pine stands, nevertheless the contribution of other factors will turn the sites into non-suitable for growth.

Temperature is also one of the key factors effecting growth of Scots pine. Its significance is illustrated in both Figure 5.7 with the form of seasonal variation of maximum and minimum temperatures and also in Figure 5.9 in the form of seasonal frost days. Winter maximum temperatures appeared to have affected positively both production of timber and ecosystem carbon sequestration. Increase in winter maximum temperature will result in a significant increase in both gross and net primary production, showing that photosynthesis during the warm winter days is more efficient. Apparently maximum temperatures during winter time are closer to the optimum temperatures for growth of Scots pine having a significant increase in production. However, increase in production will increase also the loss of carbon through autotrophic respiration. During summer, increase in maximum temperatures will limit growth as values over exceed optimum temperatures for growth, causing a stomata closure to reduce carbon and water losses significantly reducing growth. Interestingly, an increase in tempera-

ture triggers belowground allocation with the greatest effect from winter temperatures, while aboveground allocation is restricted both during the winter and summer period.

On the other hand, maximum winter temperatures did not had any significant effect on heterotrophic respiration suggesting that ecosystem carbon losses during winter are mainly due to autotrophic respiration. However, during the summer period an increase in maximum temperature will cause a decrease in both heterotrophic and autotrophic respiration as stomata will close to avoid further water loss, and although the decrease of productivity is expected the reduction of heterotrophic respiration is something that contradicts recent studies showing a relationship between increased soil respiration and rising temperatures (Zerva *et al*., 2005).

Winter precipitation had a greater effect than summer precipitation (Figure 5.8). Increasing winter precipitation limited production, while summer precipitation supported growth. During winter, precipitation increases soil capacity and when water holding capacity is exceeded they become water logged. When photosynthesis stops, water uptake is also stopped causing the death of the roots due to water logging. In Chapter 3 a similar restriction of growth was highlighted but with precipitation during late spring. However, a better look into the precipitation component factors of the spatial PCA shows that what was denoted as winter precipitation includes also some of the spring months. Considering the finding in Chapter 3 the observed restriction of ”winter” precipitation could be actually a restriction by spring precipitation. Precipitation was found to be significantly low during the spring months (see Chapter 3) allowing freely drained soil to lose any water captured during the winter. However, when summer photosynthesis starts water is limited due to stomatal closure until summer precipitation ”fill up” the water table causing nevertheless significant growth limitation.

Greatly important was the number of days when frost occurred. The results suggested that winter frost is having a significant impact on photosynthesis. However, findings in Chapter 3 showed that photosynthesis is taking place even during the winter months. Thus, it is not the actual effect of frost that has an impact on growth but the fact that photosynthesis stops during those days when temperatures are very low. For that reason summer frost does not appear to have any significant effect on growth. Sunshine on

the other hand is undoubtable a huge significant contributor to growth. Interestingly, increased summer solar radiation will increase decomposition of labile litter in the soil, increasing also respiration losses, however the same does not apply for refractory and humified soil carbon, which appeared to have no effect from solar radiation.

Many previous studies identified the effect of temperature and rainfall on Scots pine growth either in Europe (Corona *et al*., 1998; Fries *et al*., 1998; Tegelmark, 1999) or Scotland (Cook *et al*., 1977; White, 1982a,b; Tyler *et al*., 1996). The importance of temperature and rainfall on site index and thus height development is also well documented for many species (Klinka and Carter, 1990; Milner *et al*., 1996; Corona *et al*., 1998). Zianis and Mencuccini (2005) showed the relation of aboveground productivity with elevation although the study did not find any relation between leaf area index and elevation. However, the change in tree allocation due to mechanical reasons caused by strong winds was also discussed. Our model findings support the hypothesis that belowground allocation changes with mechanical pressure. The altitudinal decline of Scots pine growth was also demonstrated from the study by James *et al*. (1994), which shows that valleys are more productive and also that a sharp decline was observed at the tree-line.

Winter temperatures were also found to be more important than precipitation for Scots pine ring growth (Grace and Norton, 1990). Winter browning or frost drought was suggested being the reason for the strong correlation with winter temperature, which seems to come in perfect alignment with our findings.

Our findings also suggests that a change in climate will have a great impact on Scots pine growth. Kellomäki and Kolstrom (1994) showed that a possible climate change scenario with increased temperature will cause an increase in stem growth for stands in northern Finland, but continued increase in temperature will finally end up in a rapid decrease. Kirschbaum (2000) supports Kellomäki and Kolstrom (1994) views by suggesting that although trees are adaptable to high temperatures, increase temperatures will increase vapour pressure deficit and will increase transpiration rate. The increase in CO_2 will cause the stomata to close and decrease respiration, in particular maintenance respiration (Kellomäki and Kolstrom, 1994), while the increased precipi-

tation, which is also a part of a climate change scenario, will not be adequate enough to cause stomata to open and assimilate the excess CO_2 (Kirschbaum, 2000), reducing growth. Air pollution on the other hand, is well known causing an increase in nitrogen deposition having a significant effect on forest growth. Cannell *et al.* (1998) investigated the effect of CO_2 temperature and nitrogen deposition effect on timber growth for conifers in the UK. The results showed that combined the three possible scenarios, timber growth will only increase 0.5 $m^3\ ha^{-1}\ yr^{-1}$ per decade, where as the effect only of nitrogen deposition or increase CO_2 will add a 14% in current growth rates. Cannell *et al.* (1998) also supports the findings by Kellomäki and Kolstrom (1994) showing that increasing temperature combined with increase in CO_2 will have restricting effect on growth. The most singificiant increase however, was caused by a combined effect of increasing nitrogen and CO_2 with effect also in leaf area index and forest biomass. Our findings supports the effects of such climate changes scenarios, although it was not investigated.

Vucetich *et al.* (2000) found a latitudinal gradient in ecosystem carbon pools from a range of Scots pine sites including countries like Poland, Lithuania, Latvia, Estonia and Finland. The study found that carbon sequestration, decomposition rates and litterfall decreased non-linearly with increasing latitude due to decline in temperature and precipitation. Although latitudinal differences are significant for Scots pine growth, this was not the case for Scotland due to very short range. However, the significant differences between north and south in evapotranspiration rates are expected to be mainly due to temperature and precipitation differences (Figure 5.1). Nevertheless, very interesting is the fact that east and west differences are clear even for the northern parts of Scotland (Figure 5.12). However, model results comes into agreement with results in Chapter 6 that nitrogen uptake becomes limited for stands with higher altitude.

Temperature and site fertility effect are also reported to affect growth of Scots pine by Fries *et al.* (1998), while White (1982a,b) reports that Scots pine growth in Great Britain is mainly associated with incoming solar radiation, soil texture and soil moisture content. Summer solar radiation was found to be very important for growth (Chapter 3) and carbon accumulation.

The effect of rising temperature above a certain optimum is illustrated by Grant (2004), which study showed that influxes of CO_2 stopped when day temperature rose above 25°C. The study showed that increase in temperature will cause lower water potentials, which is forced by large vapour pressure deficit, whereas carbon efluxes rose with increased temperature. The study also showed that net primary production and carbon accumulation for upper-slope stands of black spruce was more than twice of stands at the bottom of the basin. High slope stands were exposed more to solar radiation reducing soil water content, increasing soil temperature, decomposition and so heterotrophic respiration, while it had more rapid oxygen uptake due to large nitrogen mineralisation and uptake. Upper slope sites although they consist from podzolic and brown earth soils (Chapter 3), consistent precipitation through out the year will water log soils and run off will occur. Water logged soils in combination with low temperature will reduce heterotrophic respiration and decomposition which will make nitrogen mineralisation not adequate enough for sufficient growth.

5.4.2 Understanding the spatial patterns of Scots pine productivity

During the process of mapping potential productivity for a species, it is very important to completely understand its spatial patterns and to identify the major contributors for a specific pattern. Modern spatial analysis techniques available in any commercial geographical information system package can provide adequate answers. Spatial regression analysis and autocorrelation analysis in this study were used to understand how randomised or clustered the patterns of Scots pine productivity were so as to help identify those topographic or climatic factors responsible for this patterns. Additionally, regression analysis gave a further statistical understanding into the temporal changes of spatial patterns.

Values of Moran's I statistic close to unit clearly indicate that patterns for most variables are well clustered. Refractory and humified carbon stocks appear to be not very well clustered, which means that there are no clear regions where values are similar. This makes harder the identification of the parameters responsible for the patterns. Although correlation analysis gave an indication of the climatic or topographic effect on

soil stocks, the spatial variability is also very high. Looking at young labile carbon in the soil (Figure 5.4) it shows a different picture. The high autocorrelation suggests that a map of the easily decomposed carbon in the soil will look more fragmented. Correlation analysis showed there was a significant correlation with temperature and so it is expected that its spatial patterns (Figure 5.1) will follow those of temperature. However, regression analysis using a single parameter linear comparison did not find any significant relation with neither maximum winter, maximum summer or minimum winter temperature, suggesting that multiple parameters result to its patterns.

Nevertheless, regression analysis did show a few significant single parameter linear relationships. Patterns of mean annual increment (Figure A.5) are strongly influenced by those of minimum winter temperature. Correlation analysis showed that there is a strong correlation between the two. The fact that there is a strong linear relationship between the two standardised variables (Figure 5.11) shows that minimum temperature patterns affect those of MAI in the first few years since Scots pine's establishment. However, this relationship becomes weaker as stands grow older (Figure 5.11 and Table 5.1). Other parameters such as solar radiation, available nitrogen, soil water availability or frost days contribute so as to turn the linear relationship into a multivariate. For such an occasion, a further investigation is needed applying a multiple linear model. Patterns of annual transpiration are also strongly related to maximum winter temperatures which becomes weaker for older stands. Table 5.1 also shows that minimum winter temperature is highly responsible for autotrophic respiration pattern for the whole 100 years of the simulation period. The relationship is stronger when stands are young (χ^2 = 389.55), while its strength is reduced as the stands gets older but significantly close to the 1:1 relationship. That clearly indicates autotrophic respiration patterns (Figure A.3) are depended on minimum winter temperature, which also can be translated as a significant effect on net primary production's spatial patterns (Figure A.2).

Figure 5.5 also showed that net ecosystem's productivity spatial autocorrelation is temporally extremely variable. This means it is really difficult to distinguish regions of high and low ecosystem carbon accumulation for the early stages of Scots pine life,

whereas patterns become more clear as the stands grow older. This regionalisation is missing for the first twelve to fifteen years, while it happens suddenly and within ten years. It is not very clear why this extreme clustering of the values occurs. A possible explanation however, is that Scots pine stands can be carbon sources in average up to 16 years, with 12 years for high productivity stands and 17 years for low productivity (Chapter 6), which is also supported by Wirth *et al.* (2002) that shows Siberian Scots pine on fertile sites becoming a sink at the age of 12. In Chapter 6 it was also found that maximum leaf area occurs from 24 years for the high productivity stands up to 34 years for the low productivity stands since establishment, timing which matches the 30 years necessary for the complete clustering of $P_{E_{AC}}$ suggesting that canopy closure will stabilise patterns of photosynthesis, therefore carbon production. The above in combination with the fact that autocorrelation of $P_{E_{AC}}$ changes slightly, until it reaches the age of 90, time approximately at which carbon production becomes equal to respiration losses (Chapter 6), leads to the conclusion that the unclustering of the first twelve years is due to higher than production respiration losses. After 90 years, patterns of carbon accumulation became again unclustered as respiration again exceeded production. A general conclusion is that respiration is spatially highly variable, explaining the highly randomized spatial patterns of $P_{E_{AC}}$. Observing the autocorrelation index for both R_E and R_H in Figure 5.5 it is clear that heterotrophic respiration does not exceed 0.8 suggesting a not well fragmented pattern.

Regression and autocorrelation analysis gave a quick and reliable understanding of the variables responsible for the observed patterns of productivity. However, a visual inspection of the produced maps could sufficiently lead to some more conclusions. Figure 5.12 and 5.13 give predictions of maximum MAI and maximum $P_{E_{AC}}$. Observing the patterns for maximum MAI, four major regions could be distinguished. Those regions have a circular form with the highest value regions including all south-east and south-west coasts, while the lowest value regions include all mountain regions of Cairngorms, Ben Nevis and western coast of Scotland, including also the central mountainous region of the lowlands next to the borders with England. Observing maps of temperature, precipitation and elevation (Figure 5.2 and 5.1) it is clear that current patterns of timber increment are mainly effected by topographic parameters such as el-

evation, and climatic parameter such as precipitation, solar radiation and temperature. Although correlation analysis did not show a very strong correlation of MAI with solar radiation or precipitation a visual inspection of the maps shows the central western region of Scotland is potentially unsuitable for timber production as increment is very low (3-4 $\mathrm{m}^3\ \mathrm{ha}^{-1}$).

Although no information of water potentials or soil water availability were available for comparison with productivity outputs, astonishing are the similarities with a map of potential water deficit (mm) from Birse and Dry (1970) (Figure 5.14). The map illustrates the regions in Scotland which are clearly not limited in water. Those regions include the east mountains of Cairngorms, the western coast of Scotland from south-west up to north-west and the central mountain region close to the borders with England. The eastern coast had the greatest water deficit including coastline from the south up to Moray coast and the wider Inverness area. Interesting is that the north-east side of Scotland, further north from the city of Inverness appears to have a greater deficit. The striking similarities with 3-PGN SPATIAL predictions of potential MAI and $P_{E_{AC}}$ shows the significance role of soil water for Scots pine growth.

5.4.3 Carbon and timber productivity of Scots pine

In this study the scenario for estimating the potential productivity of Scots pine in both terms of carbon and timber yield was based on non-changeable climatic scenario, where climate is following the average values for the period between 1961 - 1990, whereas the initial state of soil carbon balance follows the base line of 1990 provided by our soil data. It was also assumed that Scots pine stands exists in all the extent of Scotland, which certainly has driven the model in producing unrealistic values of accumulated net ecosystem productivity and mean annual increment for certain regions. Values that range outside the well known range of productivity for Scots pine were considered as an indication of non-suitability of the site for growth. For example, in Figure 5.13 values of maximum $P_{E_{AC}}$ reached as low as -23 $\mathrm{tC}\ \mathrm{ha}^{-1}$. These regions include the high elevation mountain regions of Scotland in the central belt and southern mountain region, which is well know that Scots pine does not grow. However, it

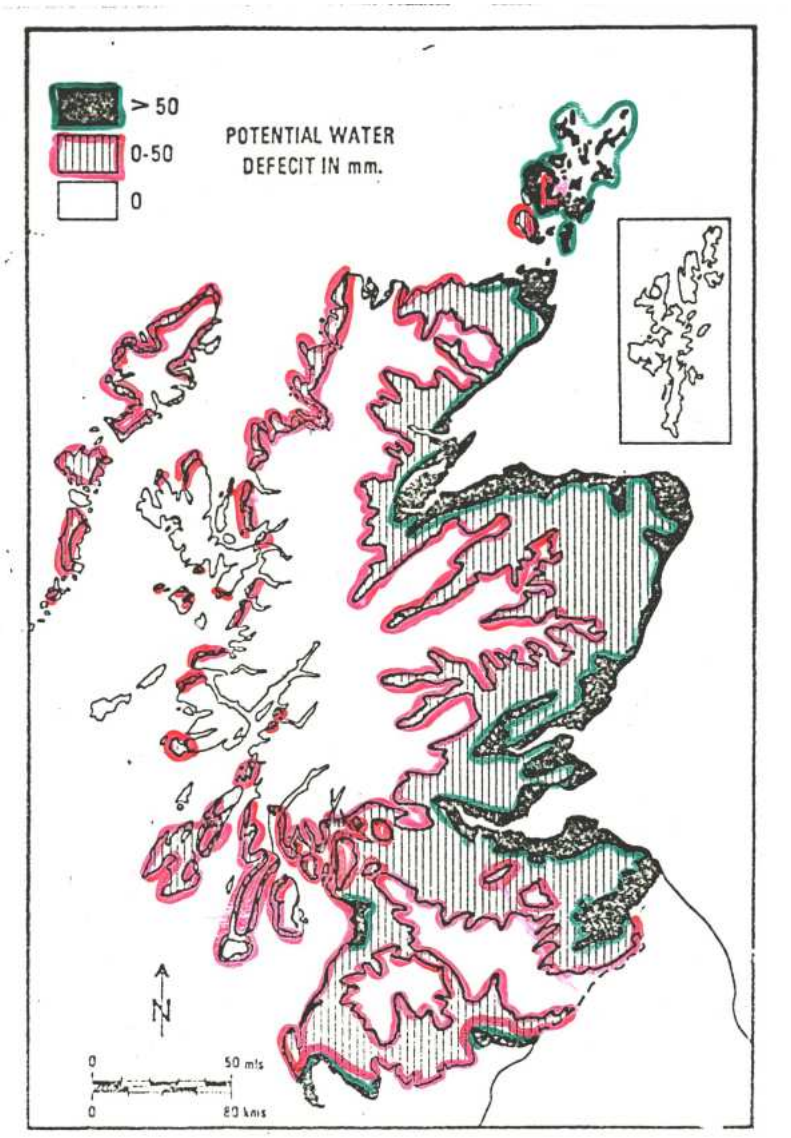

Figure 5.14: Potential water deficits in Scotland as it was given by Birse and Dry (1970)

is known that an overestimation of the carbon balance could be due to unsuitability of soil information. Soil carbon balance and texture information came from a European study, which is in its early stages. The methodology for deriving top soil organic content is well tested, however, the sample size was small introducing an uncertainty not considered, which has been added into our predictions for both ecosystem carbon balance and timber production.

Model predictions of P_E for 25 year old stands come in good agreement with Gower *et al*. (2001) who gave an estimation of 2.45 $\mathrm{tC\ ha^{-1}\ yr^{-1}}$ for Siberian Scots pine.

The same authors gave a prediction of 2.60 $\mathrm{tC\ ha^{-1}\ yr^{-1}}$ for the same stands which falls well within our model's predictions. On the other hand, Zheng *et al*. (2004) gave a range for P_N in Finland between 1.72 to 10.91 $\mathrm{tC\ ha^{-1}\ yr^{-1}}$, with a mean of 4.08 $\mathrm{tC\ ha^{-1}\ yr^{-1}}$.

The model also came in good agreement with data by Kolari *et al*. (2004) who estimated that 40 years old Scots pine in Finland had an ecosystem productivity between 2.14 - 2.42 $\mathrm{tC\ ha^{-1}\ yr^{-1}}$, whereas older stands (75 years old) produced 2.52 $\mathrm{tC\ ha^{-1}\ yr^{-1}}$, with an average of 1.085 $\mathrm{tC\ ha^{-1}\ yr^{-1}}$ for the whole life of the stand. On the other hand, Borghetti and Magnani (2003) gave 1.69 $\mathrm{tC\ ha^{-1}\ yr^{-1}}$ for 39 year old stands and 3.02 $\mathrm{tC\ ha^{-1}\ yr^{-1}}$ for 75 year old stands in Finland, whereas Scots pine in Sweden had net ecosystem production of 4 $\mathrm{tC\ ha^{-1}\ yr^{-1}}$ for 36 year old stands and 3.8 $\mathrm{tC\ ha^{-1}\ yr^{-1}}$ for 68 year old stands. Moreover, Markkanen *et al*. (2001) estimated that minimum P_E for boreal Scots pine was 1.65 $\mathrm{tC\ ha^{-1}\ yr^{-1}}$ whereas the maximum was 3.04 $\mathrm{tC\ ha^{-1}\ yr^{-1}}$. Model range fell well within the range of all this studies.

In Britain however, a 71 year old, yield class 10 Scots pine stand had P_E of 2.27 $\mathrm{tC\ ha^{-1}\ yr^{-1}}$, whereas the total accumulated carbon stored in the ecosystem reached 178 $\mathrm{tC\ ha^{-1}}$ (Cannell and Milne, 1995). Model predictions for P_E for young stands in Scotland are close to lower published values for Finish stands but for older stands. Additionally, model predicted that after 50 years P_E reaches values between 0.5 - 1.08 $\mathrm{tC\ ha^{-1}\ yr^{-1}}$. Considering that estimations of P_N are closer to reality, the conclusion is that heterotrophic respiration could be overestimated, resulting into underestimation of net ecosystem productivity. Soil respiration in 3-PGN SPATIAL is based on the decomposition rates and on steady state soil carbon pools, which it was shown to produce reasonable results Chapter 6. Bellamy *et al*. (2005) on the other hand, showed that highly organic soils in England and Wales had a loss of carbon in average more than 2% a year with almost 1% loss per year for coniferous woodlands. Although climatic differences may be significant between Scotland and England, a better look at the Scottish soil organic carbon map shows that areas with negative P_E are those with high organic carbon content soils. However, this is not quite clear from our simulations, as ecosystem respiration (Figure A.3) ranged between 7.17 - 9.39 $\mathrm{tC\ ha^{-1}\ yr^{-1}}$,

which is reasonably close to estimation by Borghetti and Magnani (2003) for Finish stands with 8.64 $\mathrm{tC\,ha^{-1}\,yr^{-1}}$ for a 39 year old stand. Further investigation is needed into why 3-PGN SPATIAL underestimates P_E only into some regions.

As model predictions for yield class were difficult to produce, the next closest variable was maximum MAI (Figure 5.12). Although maximum MAI is not always close to yield class, its values showed an underestimation in yield potentials. This underestimation again could be either due to calculation error of the model or effect of the initial soil state variables. Yield classes range from 6 up to 14 $\mathrm{m^3\,ha^{-1}}$ (Chapter 3). The range however of estimated volume increment for 39 Scots pine stands around Scotland using ESC was shown to be between 4 and 10 $\mathrm{m^3\,ha^{-1}\,yr^{-1}}$ with an average of 7.3 $\mathrm{m^3\,ha^{-1}\,yr^{-1}}$ ($\pm\,1.6$) (Chapter 3), which is significantly close to our predictions. The fact that one empirical and one process-based model gave so close predictions suggests that a bias was quite possibly introduced during the estimation of yield class from field data.

5.4.4 Classification based on carbon sequestration or timber increment potentials?

Site classification so far was based on timber increment. Yield class is widely used in forestry as an indication of site potential timber productivity. Nowadays, the new role of forest, that of carbon sequestration, which came with the adoption of the Kyoto protocol increased the need for site classification in terms of carbon accumulated. However, research in modelling of the spatial variations of forest productivity have failed to provide adequate site classification for decision making. The first effort for a spatial classification scheme in Great Britain was the Ecological Site Classification (ESC, Pyatt *et al*., 2001) and its spatial version (Ray, 2001). ESC is a decision support system (DSS), which provides estimates of potential timber production of any site, even when a forest does not exists, based on a series of soil information inputs provided by an extensive soil survey and phytosociological relations. Species survey combined with information about soil texture, root depth, stoniness and parent material provide estimates of soil moisture and nutrient regimes, which later are combined with

climatic inputs such as accumulated temperature above 5°C, moisture deficit, windiness and continentality. ESC has been integrated with ArcView GIS and its capable to provide spatial estimations of soil moisture and soil nutrient regime, which then are translated into potential volume increment. Suitability of all major commercial species could also been investigated based on existing vegetation communities and the effect of temperature, precipitation and wind on growth.

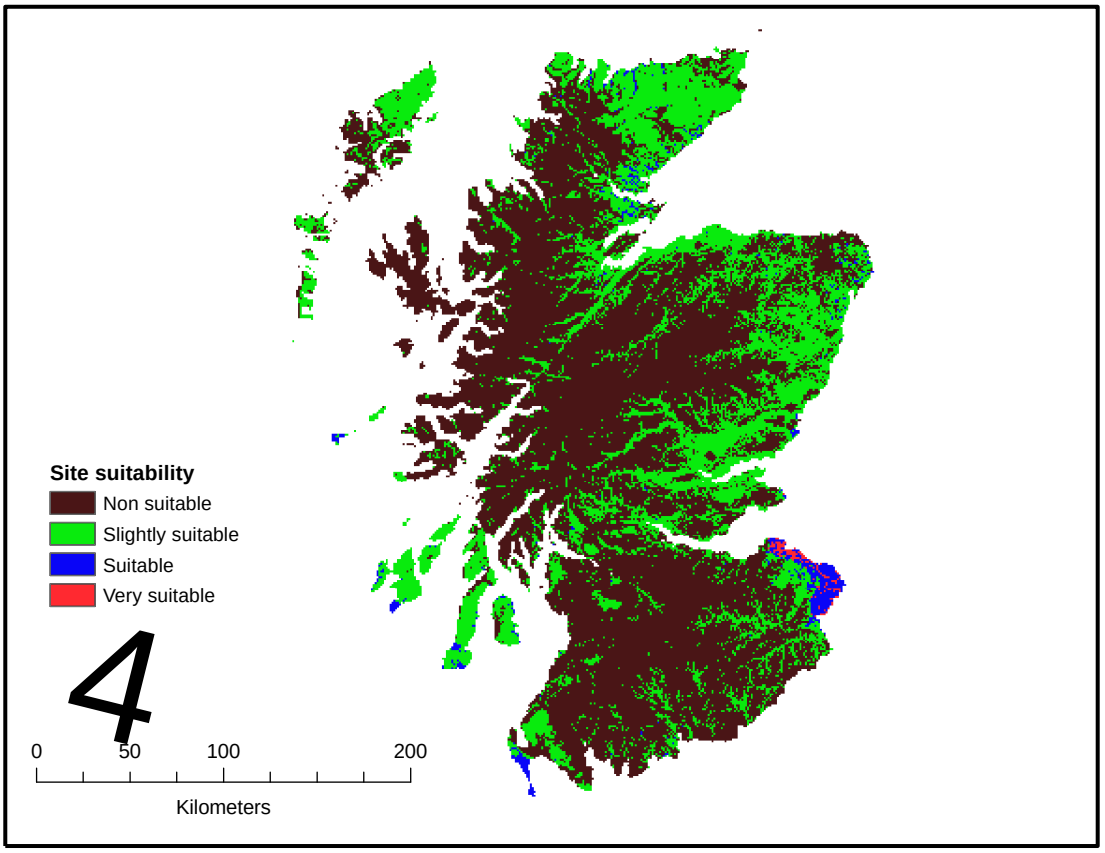

Figure 5.15: An example of potential development of a site classification scheme utilising outputs of 3-PGN SPATIAL and climatic information. The map illustrates site suitability for Scots pine plantations that produce maximum MAI greater or equal to 8 $\mathrm{m}^3\ \mathrm{ha}^{-1}\ \mathrm{yr}^{-1}$, maximum $P_{E_{AC}}$ greater or equal to 100 $\mathrm{tC\ ha}^{-1}$, while the DAMS windiness score (Pyatt *et al.*, 2001; Ray, 2001) is less or equal to 12.45. Smaller values of DAMS windiness score indicate lower wind exposure. Data were provided by Forest Research of Forestry Commission UK.

ESC is a very useful tool for forest management decision, however its potential is limited firstly because any estimations of potential site productivity are based on empirical relations with climatic and edaphic factors and secondly because no information about forest potential carbon accumulation are available. Classification with 3-PGN SPATIAL on the other hand, is possible for both aspects of forest management. Figures

5.12 and 5.13 are examples of models predictions for potential volume increment and carbon sequestration. Map algebra algorithms can be developed utilising not only input maps of potential maximum volume increment and maximum carbon sequestration but also combining climatic inputs such as windiness. When for example a strategic objective is set to identify potential planting areas for establishing commercial plantation maximizing both carbon sequestration and timber production and also avoiding any losses by wind damages then classification based on 3-PGN SPATIAL outputs is relatively straight forward. The results of the scenario are illustrated by Figure 5.15.

Classification does not have to be based any more on a single parameter, either carbon assimilation or timber production. The bringing of process-based models into site classification has open the potentials for more accurate and purpose driven classification. Simplified process-based models such as 3-PGN SPATIAL could provide a large array of variables for developing multivariable classification algorithms based either on soil carbon and nutritional status, ecosystem carbon assimilation, timber production, or leaf area index, combined with a series of environmental, topographic or land use variables. The advantage of such a classification strategy is that it is adaptable to any specific management objective, providing specific classification for specific objectives and finally because classification becomes adaptable to any future climatic or environmental changes e.g., climate change, change in land use or geomorphology. The integration with a GIS framework gives a DSS capable for fast and reliable mapping. Future development however, should also include web-based GIS framework for process-based classification utilising the advantage of remotely sensed inputs.

5.5 Conclusions

To summarize the study's findings, potential productivity of Scots pine was Scotland is highly regionalised with a clear pattern between east and west. Western regions of high precipitation and low incoming solar radiation are not suitable for growth, while maximum and minimum temperatures during the winter months and the number of days with low temperatures, are having a great impact on productivity and its spatial

patterns.

Integration of the full ecosystem, simplified process-based model 3-PGN with GIS provided a tool not only into investigating the main topographic and climatic effects on physiological growth of Scots pine, but also provided a tool for advanced spatial analysis techniques, which helped mapping spatial patterns of forest production and understanding the factors responsible. Additionally, it provided a tool for site classification based on maximum volume increment, maximum ecosystem carbon accumulation and climatic effect such as wind exposure. A way forward should be the inclusion of a process-based model such as 3-PGN, with a gap model for simulating both potential patterns of productivity and natural regeneration. Their integration under a web-based GIS framework and the utilisation of remote sensed inputs of leaf area, should provide the opportunity for a classification scheme based on advanced spatial analysis techniques, capable to include any possible climatic and management effects.

CHAPTER 6

Carbon sequestration of Scots pine under normal yield production: an analysis using the process-based model 3-PGN

6.1 Introduction

At a time when carbon mitigation can help reducing atmospheric concentration of CO_2, forests of the boreal and temperate region have assumed an even increasingly important role. Knowing the current and future potential for carbon storage by these forests is key to the formation of successful environmental policies and is a major piece of information management to help define suitable strategies.

Since the end of the second world war, British forest cover has expanded about 11.8% of the land area (about 17% in Scotland), supporting approximately 20% of the current needs of the timber market. This production is based mainly on fast growing monoculture plantations of Sitka spruce, which cover about 29% of the forest/woodland area in Britain (and 47% in Scotland) (Forestry Statistics, 2006). Other coniferous species include Scots pine, European larch, lodgepole pine and Douglas fir. Scots pine is native to Scotland where it covers an area of about 140,000 of semi-natural woodlands (Mason *et al*., 2004) and 219,000 hectares of monoculture plantations (Forestry Commission, National Inventory of Wooldlands and Trees, 2003).

The distribution of Scots pine in the boreal and temperate region extends from Siberian Russia, to Sweden, Norway and Finland, China and Great Britain (Gower *et al*., 2001;

Schulze *et al*., 1999). Within Europe Scots pine could also be found in many regions of Central and Mediterranean Europe and countries such as Italy, France, Spain and Greece. This wide distribution makes it an important species in an international for forest policies, thus a knowledge of its current timber yield and carbon sequestration potential is vital.

Aboveground net primary production of Scots pine in Russia is estimated to range from as low as 0.6 to 6.7 $\mathrm{tC\ ha^{-1}\ yr^{-1}}$, whereas belowground is between 0.678 and 32.15 $\mathrm{tC\ ha^{-1}\ yr^{-1}}$ (Gower *et al*., 2001). Wirth *et al*. (2002) on the other hand, estimated net ecosystem production of 6.1 $\mathrm{tC\ ha^{-1}\ yr^{-1}}$ for the same region. Oleksyn *et al*. (2000) reported aboveground net primary production ranging between 19.2 and 50.1 $\mathrm{tC\ ha^{-1}\ yr^{-1}}$ for North European populations, 40.3 to 72.5 $\mathrm{tC\ ha^{-1}\ yr^{-1}}$ for Central European populations and 9.4 to 17.5 $\mathrm{tC\ ha^{-1}\ yr^{-1}}$ for South European populations. Borghetti and Magnani (2003) estimated Scots pine net ecosystem production of about 3.8 $\mathrm{tC\ ha^{-1}\ yr^{-1}}$ in Sweden and 3 $\mathrm{tC\ ha^{-1}\ yr^{-1}}$ in Finland, while Kolari *et al*. (2004) gives an estimation of about 2.52 $\mathrm{tC\ ha^{-1}\ yr^{-1}}$ for Southern Finland. Gross photosynthetic production of Scots pine in Europe varies between 18.83 and 30.79 $\mathrm{tC\,ha^{-1}\,yr^{-1}}$ (Berninger, 1997). When Scots pine grows older than 100 years old then net ecosystem production becomes as low as 0.1 $\mathrm{tC\ ha^{-1}\ yr^{-1}}$ in Sweden (Borghetti and Magnani, 2003) and 0.19 $\mathrm{tC\ ha^{-1}\ yr^{-1}}$ in Siberia (Wirth *et al*., 2002)

Carbon stocks of British vegetation is estimated to be 113.8 million tC of which about 80 per cent is in forest and woodland ecosystems (Cannell and Milne, 1995). Of the total carbon stored in vegetation, 25.4% is in conifer woodlands, 46.8% in broadleaved woodlands and 8.5% in mixed woodlands. Carbon stocks in Scots pine woodlands on the other hand, are estimated to be 7.1 tC, that is, 7.7% of the total carbon stored in woodlands (Cannell and Milne, 1995). Currently, forests in Great Britain appear to sequester 1.5 - 1.7 million $\mathrm{tC\ yr^{-1}}$ in trees, 0.3 - 0.5 $\mathrm{tC\ yr^{-1}}$ in litter and 0.5 $\mathrm{tC\ yr^{-1}}$ in woodproducts (Cannell and Milne, 1995).

Natural and semi-natural Scots pine woodlands of Scotland, have been historically managed as high forests of even aged stands, sometimes mixed with birch and other broadleaves. Clearfelling, seed trees and shelter-wood systems were the most impor-

tant silvicultural systems applied. Their management objectives currently include conservation and secondly timber production and recreation. However, in the commercial plantations managed mainly for timber production clearfelling is the main silvicultural system applied, while other silvicultural practices such as thinnings and fertilisation are also applied (Mason *et al.*, 2004). In native woodlands the yield class ranges between 4 and 10 $\mathrm{m}^3\ \mathrm{ha}^{-1}\ \mathrm{yr}^{-1}$, with the poorest sites only marginally suitable for any sustainable management. Age of maximum mean annual volume increment ranges between 100 for yield class 4 and 70 years for yield class 10 (Mason *et al.*, 2004). Although yield tables predict timber production for Scots pine up to yield class 14, this is highly unlikely even for commercial plantations (Chapter 3).

6.1.1 Objectives of the study

Following the adoption of the Kyoto protocol, new strategic planning for forest ecosystems should consider forests as a significant carbon sink. Until recently, the majority of forest plantation and woodland were managed based on their economic return, which focuses on maximizing timber yield. As carbon sequestration becomes a key management objective, information are necessary about the impact of current forest management practices on ecosystem carbon. In the current study, the process-based model 3-PGN was deployed to provide answers to questions such as how much carbon is sequestered when silvicultural treatments target the achievement of normal yield established by yield tables and what is the deviation from those normal conditions with different site conditions. Finally, we provide a discussion on which is the optimum management decision, timber production or carbon sequestration and for which rotation length.

6.2 Materials and methods

6.2.1 The 3-PGN model

3-PGN (3-PG Nitrogen) is a two-way dynamic integration of the simplified process-based model 3-PG (Landsberg and Waring, 1997) and the equally simplified soil organic matter model ICBM/2N (see Chapter 4). 3-PG is a well established model for simulating forest production based on basic physiological principles of growth. It has been applied successfully in a wide range of biomes and climatic conditions including Eucalyptus plantations (Tickle *et al*., 2001a; Sands and Landsberg, 2002; Coops *et al*., 1998), rimu (*Dacrydium cupressinum* Solander ex G. Forst., White *et al*., 2000; Whitehead *et al*., 2002), tropical species of the Amazon basin (Hirsch *et al*., 2003, 2004; Stape *et al*., 2004) and many conifer species such as lodgepole pine (*Pinus patula* Schlecht. and Chamisso, Dye, 2001), Sitka spruce (Waring, 2000) and most recently Scots pine in Finland (Landsberg *et al*., 2005). Tickle *et al*. (2001a,b), Landsberg *et al*. (2003) and Coops *et al*. (1998, 2001a,b) demonstrate the application of 3-PG at a regional scale utilizing spatial data derived from remote sensing and Geographical Information Systems (GIS).

ICBM/2N on the other hand (Andrén and Kätterer, 1997) has been successful in many agriculture studies (Andrén *et al*., 2001; Kätterer and Andrén, 2001, 1999). Kätterer and Andrén (1999) used ICBM to investigate the influence of management on soil carbon stocks for agricultural fields in Northern Europe, whereas Andrén *et al*. (2001) used ICBM to investigate the influence of soil fauna on soil carbon balance. Finally, Kätterer and Andrén (2001) used the ICBM family in a series of experiments to evaluate their use.

3-PGN uses a simplified radiation absorption model, which converts absorbed photosynthetically active radiation calculated from incoming solar radiation into gross primary production by multiplication with the quantum yield efficiency. A series of climatic, soil and age modifiers reduce maximum quantum yield efficiency to account for the effect of environment on photosynthesis. Modifiers are calculated from mean

monthly values of temperature, vapour pressure deficit, precipitation and incoming solar radiation, with their values ranging from 0 to 1. Physiological effects on photosynthesis, are also accounted with a physiological modifier. Net primary production is derived from gross primary production assuming a fixed ratio to account for respiration losses (Landsberg and Waring, 1997; Waring *et al.*, 1998). Then biomass is partitioned into three structural components including stem, foliage and root with allocation firstly directed to roots after estimation of the influence of soil nutrition and soil water. Soil water balance is derived from the balance of the incoming precipitation, canopy interception and transpiration using the Penman - Monteith formula (Landsberg and Waring, 1997), while leaf area index is the product of an age-depended specific leaf area and current foliage biomass. Litterfall is estimated based on a time depended litterfall rate, while natural morality is accounted for using the self thinning law. The option of thinning is represented based on the percentage of biomass relative to the biomass of the average tree.

3-PGN has two carbon pools, one ”labile”, which includes the fine woody debris and one ”refractory” with lower decomposition rate, which include coarse woody debris. There is also one old pool, which represents the humified organic matter. Equal number of pools exist for soil nitrogen. Decomposition rates are linearly related to temperature and soil water. Fertility rating, which is still utilized by 3-PGN is estimated as a ratio between the availability of nitrogen in the soil and the uptake of nitrogen by the stand based on its growth potential assuming nitrogen is the most significant element for growth (see Chapter 4). Nitrogen availability, which represents the amount of nitrogen in a mineral form is estimated as a by-product of the process of litter decomposition from ICBM/2N’s nitrogen pools with the assumption that lost of nitrogen through leaching is negligible. Nitrogen uptake, is estimated as the stand’s nitrogen demand depended on foliage growth rate and foliage nitrogen concentration, making nitrogen uptake linearly depended on the growth capacity of the stands on the previous time step.

6.2.2 Calibration and validation

The calibration was conducted with a technique based on Bayes's theorem for ecological models (Van Oijen *et al*., 2005), which makes use of modern computational capabilities by running Markov Chain Monte Carlo simulations. The Metropolis-Hastings algorithm was also adopted for minimization of computational time (Robert and Casella, 2004; Van Oijen *et al*., 2005). For more details on the procedure see Chapter 4.

6.2.3 Study area and data

The model was calibrated and validated for monospecies, even-aged plantations of Scots pine (*Pinus sylvestris* L.) in Scotland, managed in their majority by Forestry Commission. Model parameters were fitted to observed data from 14 stands, six of which belong to the Forestry Commission's permanent sample plots database and eight to an extensive field sampling campaign of 45 stands across the country (Chapter 3), to ensure representativity of the majority of site conditions. The 45 sites were distributed over a range of elevations and latitudes (Figure 3.1) and they covered three main climatic zones, i.e., cool moist, cool wet and warm moist according to ESC climatic descriptions (Pyatt *et al*., 2001). Soil type varied from sandy with deep water table to deep peats, whereas ground vegetation included mosses, bracken, heather and billbery. In each plot, measurements of tree height, diameter and tree density were taken, while biomass of stem, roots and foliage was calculated using allometric equations (Chapter 3) and volume was determined using Forestry Commission's volume tariffs. The biomass initialisation of the model was based on forest management tables (Forestry Commission, Forest Management Tables, 1966). Elevational information for each plot were derived from a 50 m digital elevation model (DEM) provided by Ordnance Survey UK, while latitude and longitude information were extracted from a spatial database developed from data by the Climate Research Unit of the University of East Anglia (CRU).

6.2.4 Meteorological data

3-PGN is driven by a series of climatic variables including mean monthly maximum and minimum temperature ($^{\circ}\mathrm{C}$), mean monthly precipitation (mm), mean monthly incoming solar radiation ($\mathrm{MJ\,m^{-2}\,day^{-1}}$) and mean monthly vapour pressure deficit (mBar). Other optional inputs are rain days and frost days. Mean monthly values of all the necessary climatic variables were obtained from the Climate Research Unit of the University of East Anglia (CRU) in a 10 km point grid for the period 1961 - 1997 with a spatial distribution across Great Britain. The data set was geostatistically interpolated and reduced in a distribution covering Scotland's mainland. For each data point, values for a low, high and average elevation were available, however only values at average elevation were used to remove any elevational effect on the values of the climatic variables. Values were then extracted from the developed 1km spatial database for each calibration site, validation sites and for the 45 sites.

Incoming solar radiation on the other hand, was predicted using an algorithm utilizing mean monthly averages of air temperature, total precipitation and relative humidity (Nikolov and Zeller, 1992). The algorithm first estimates incoming solar radiation at the top of the atmosphere. The values are then reduced according to air temperature, humidity and cloudiness. Corrections for site topography and elevation were also applied using information extracted from DEM. The algorithm has been tested for the whole northern hemisphere, in a range of sites from subpolar regions to the tropics (Nikolov and Zeller, 1992). Its results were also validated for two sites in Scotland for which local data were available from meteorological station (Chapter 4). Calculations were performed with an ArcInfo workstation using the extended spatial database of mean monthly values.

6.2.5 Fitting 3-PGN with yield tables

After calibration and validation of the model, the next step involved fitting the outputs of 3-PGN to the predictions of normal yield tables (Forestry Commission, Forest Management Tables, 1966). Outputs to fit included standing volume (V, $\mathrm{m^3\,ha^{-1}}$) of

the remaining stand after thinning, mean annual increment (MAI, $\mathrm{m^3\ ha^{-1}\ yr^{-1}}$) and current annual increment (CAI, $\mathrm{m^3\ ha^{-1}\ yr^{-1}}$). However, model predictions of MAI and CAI are for the crop remaining after thinning and not for the total crop (including the increment of the timber removed by thinning), so an adjustment was necessary to correct the output of the model.

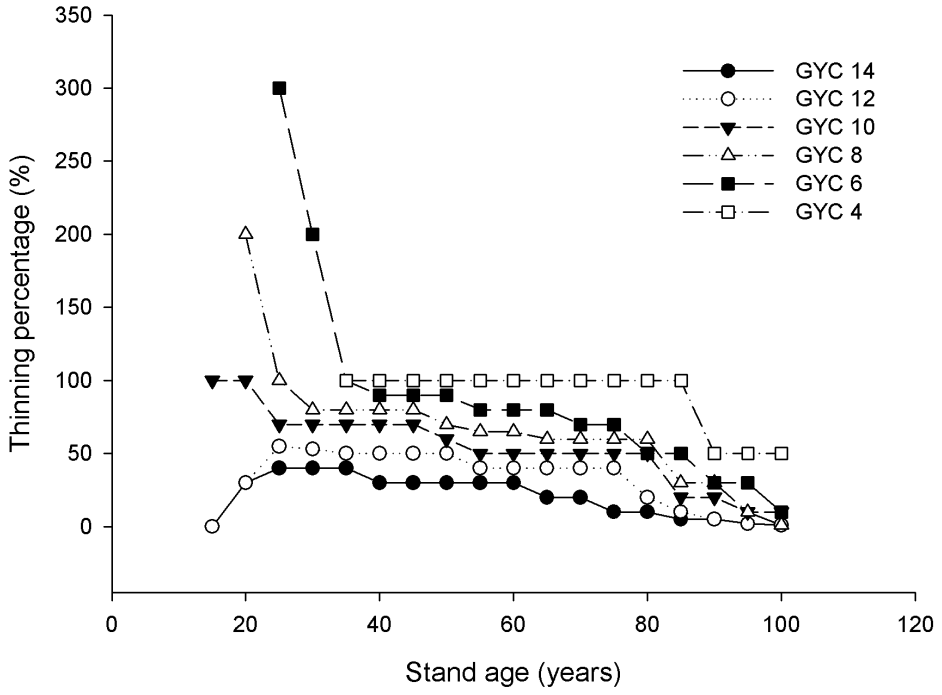

Figure 6.1: Thinning regimes used to fit outputs of 3-PGN to normal yield tables for six yield classes, expressed as a percentages of biomass removed for each structural component (i.e., stem, foliage and roots) of the mean single tree. Percentages above 100 represent thinning from above.

To test the behaviour of the model for the range of yield classes, model runs were executed for six ”mean sites”, with weather data across the 45 field sample plots grouped and averaged per observed yield class. Other inputs adjusted to represent the ”mean site” conditions per class included latitude, soil texture and maximum soil water holding capacity. Nitrogen initial state variables also varied between classes to represent differences in nutritional status. Values were set manually to values which nitrogen availability does not limit growth. Initial state variables for carbon stocks were assumed similar between classes with values representative for moorland soils (Wilson and Puri, 2001). Initial stocking was set to 5102 trees $\mathrm{ha^{-1}}$ (Forestry Commission,

Forest Management Tables, 1966), whereas initial stem, foliage and root biomass were set to 0.01, 0.1 and 0.01 respectively.

The fitting procedure included the construction of a thinning regime for 3-PGN that predicted values of stand volume, MAI and CAI matching those of normal yield tables (Figure 6.1). Timing of thinning and number of stems per hectare remaining after the event, followed the yield tables starting from the age of 15 (depending on yield class) to 100 years with 5 years intervals. The thinning regime was quantified as a percentage of the biomass removed of the mean single tree for the three structural tissues i.e., stem, foliage and roots. The initial thinning regime was taken from the yield tables and adjusted when necessary to fit the observed values of the tables. As clearly mentioned, different initial nitrogen availabilities were deployed for each class.

6.2.6 Effect of site conditions on normal production

To investigate the effect of site conditions i.e., temperature, precipitation, soil type, fertilisation or management, on normal yield and carbon sequestration under those conditions, 3-PGN was applied to the 45 field sites. For each site, meteorological data were extracted from the spatial database, whereas initial soil information came from the soil survey. Sites were divided according to their estimated (from field data) yield class and the equivalent normal thinning regime (obtained from fitting the tables) was applied. Initial soil nitrogen and carbon stocks used to fit yield tables were used to initialise the runs for each site. The simulations produced results for both timber increment and net ecosystem production. Sites then were grouped per yield class and the rotation length, calculated yield class and accumulated net ecosystem production were compared with parameters of normal yield tables and with other site factors e.g., elevation, latitude, longitude. Factors from a principal component analysis of the meteorological data with other soil and site variables, were plotted against predictions (for more details see Chapter 3). The simulation period was 100 years since planting of the stands.

6.2.7 Calculations and analysis

For each of the 45 sites and for the five yield classes, outputs of stand volume, MAI, CAI, stem, foliage and root biomass, L^*, total soil carbon and nitrogen stocks, P_N and P_G were produced. Additional outputs included annual soil respiration (R_H, $\mathrm{tC\ ha^{-1}\ yr^{-1}}$) and mean annual fertility rating (FR_{av}). Autotrophic respiration (R_A, $\mathrm{tC ha^{-1} yr^{-1}}$) was calculated as the difference between P_G and P_N and total ecosystem respiration was calculated as the sum of autotrophic and heterotrophic respiration (R_E =R_A +R_A, $\mathrm{tC\ ha^{-1}\ yr^{-1}}$) assuming that no other respiratory losses existed. Annual net ecosystem production (P_E, $\mathrm{tC\ ha^{-1}\ yr^{-1}}$) was estimated as the difference between net primary production and heterotrophic respiration.

$$P_E = P_N - R_H \tag{6.1}$$

Annual accumulated net ecosystem productivity ($P_{E_{AC}}$, $\mathrm{tC\ ha^{-1}}$) was also calculated, together with ratios of below/aboveground biomass, aboveground/total biomass, belowground/total biomass, forest/total ecosystem carbon stocks and soil/total ecosystem carbon stocks. Mean annual net and gross primary production ($\mathrm{tC\ ha^{-1}\ yr^{-1}}$), net ecosystem production ($\mathrm{tC ha^{-1} yr^{-1}}$), and heterotrophic respiration ($\mathrm{tC ha^{-1} yr^{-1}}$) were also calculated as the averages across the 100 years rotation cycle. Additionally, rotation length, MAI at the age of final cutting (i.e., yield class), age at maximum P_E and maximum accumulated net ecosystem production ($P_{E_{AC_X}}$, $\mathrm{tC\ ha^{-1}}$) was also calculated for each site.

After all simulations, results of V, $P_{E_{AC}}$, L^*, FR_{av} mean annual soil nitrogen availability and mean annual nitrogen uptake, from the 45 plots were plotted against stand age. From the broader outline of the scatter plot, the lower and the upper limits curves were drawn and the intervening space was then divided into five equi-distance bands with the width of each band proportional to stand age. The resulting yield classes were then plotted against the equivalent classes from the normal yield tables.

6.3 Results

The fitting of 3-PGN to normal yield tables for Scots pine is illustrated in Figure 6.2. Fitting the model to the highest productivity classes was relatively straightforward. Thinning regimes applied for yield class 14, 12 and 10 were all from below, with a range from 1 to 30, 1% to 50% and 10 to 100% of the mean tree biomass respectively.

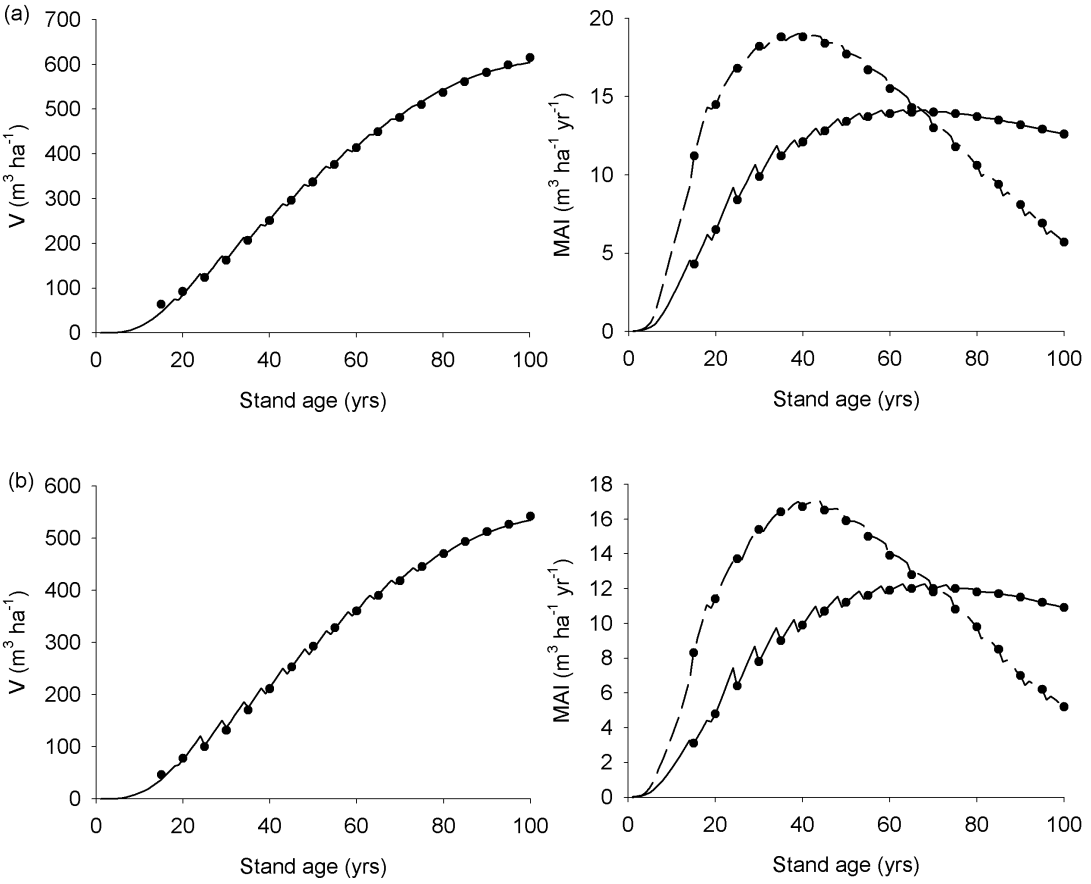

Figure 6.2: Predicted stand volume (V, $\mathrm{m^3\,ha^{-1}}$, solid lines), mean annual (MAI, $\mathrm{m^3\,ha^{-1}\,yr^{-1}}$, filed circles) and current annual volume (CAI, $\mathrm{m^3\,ha^{-1}\,yr^{-1}}$) increment against yield tables for (a) yield class 14, (b) yield class 12, (c) yield class 10, (d) yield class 8, (e) yield class 6 and (f) yield class 4. Predictions were more difficult to match given patterns for lower productivity stands.

Fitting yield classes 8 and 6 with only thinning from below was not possible. Further limitation of nutrient availability did not improve the fitting. Thus, thinning from above was applied. For yield class 6, thinning regimes reached 300% with a sharp decrease as time progressed, while for yield class 8 the maximum biomass removal reach 200% (Figure 6.1). Nevertheless, both yield classes were succesfully reproduced by

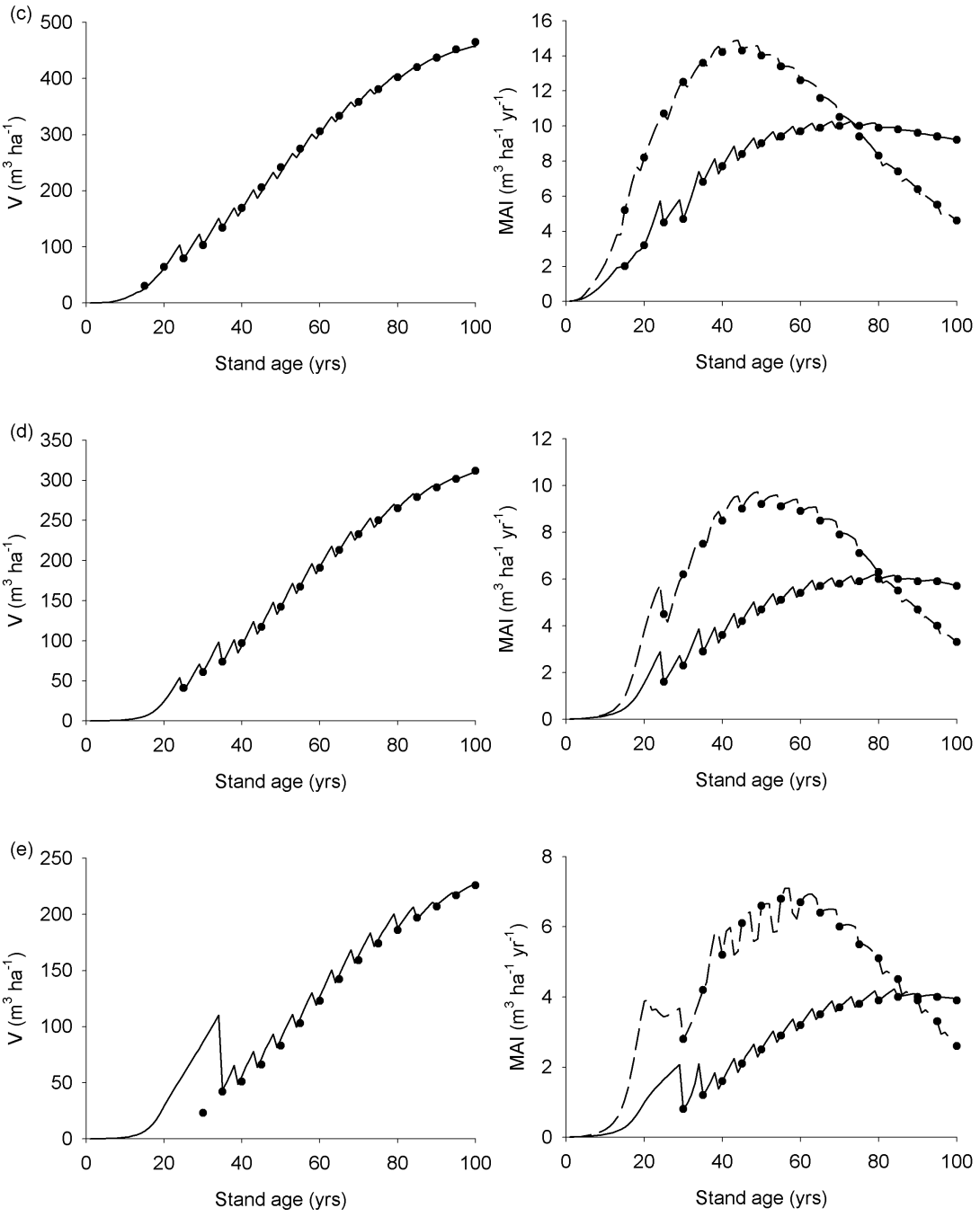

Figure 6.2: *Continued*

the model. However, a difficulty of 3-PGN to reproduce low productivity stands was observed (Figure 6.2). Although yield class was reproduced after the age of 35, it was almost imposible to produce a smoother pattern until that age. Efforts to limit further growth patterns of 3-PGN included introducing a further limitation of nutrients and soil water holding capacity, as well as applying extreme thinning from above. Fitting was

improved only with the application of thinning from above. However, the tendancy of the model to overestimate productivity of stands before the first thinning is applied was not possible to be removed for both yield classes 6 and 4 (Figure 6.2). Coefficients of determination (R^2) for stand volume ranged from 0.9227 (slope 1.0174) for yield class 4 to 0.999 (slope 1.0012) for yield class 14. Mean diameter perfectly match perfectly model's predictions with an R^2 ranging from 0.9478 to 0.9978.

6.3.1 Carbon and nitrogen, fluxes and stocks under normal yield prediction

Table 6.1 summarizes the results of fitting 3-PGN fitting to the yield tables of Scots pine. With regard to carbon fluxes, model showed that mean P_G over the simulation period ranged from 6.26 $\mathrm{tC\,ha^{-1}\,yr^{-1}}$ for yield class 4 to 8.76 $\mathrm{tC\,ha^{-1}\,yr^{-1}}$ for yield class 14 (Figure 6.3a), whereas mean P_N varied from 3.05 to 4.27 $\mathrm{tC\,ha^{-1}\,yr^{-1}}$ respectively (Figure 6.3b). Mean total heterotrophic respiration varied between 2.10 and 2.66 $\mathrm{tC\,ha^{-1}\,yr^{-1}}$ (Figure 6.3d), whereas mean total autotrophic respiration between 3.21 and 4.49 $\mathrm{tC\,ha^{-1}\,yr^{-1}}$ (Figure 6.3c). The ratio R_H/R_A varied from 0.59 to 0.66 from the highest to the lowest class. Mean annual net ecosystem productivity varied from 0.95 to 1.61 $\mathrm{tC\,ha^{-1}}$ respectively (Figure 6.3e), while for $P_{E_{AC_X}}$ model predicted values between of 95.69 to 162.16 $\mathrm{tC\,ha^{-1}}$ (Figure 6.3f), which were achieved between the ages of 91 to 93 years for yield classes 14 and 4 respectively. On the other hand, nitrogen availability varied from 0.03 to 0.28 $\mathrm{tN\,ha^{-1}\,yr^{-1}}$, while mean annual tree nitrogen uptake varied between 0.86 and 1.11 $\mathrm{tN\,ha^{-1}\,yr^{-1}}$ (Figure 6.4a and b respectively). The calculated fertility rating values (Figure 6.4c) varied with yield classes, with the first highest productivity class having values starting from 1 and decreasing up to 0.3 at about the age of 20 years, and then increasing up again around 0.5 at the age of 100. FR for the lower two lowest productivity classes started from 0 and increased up to 0.45 - 0.48.

Figure 6.3a shows the development of P_E as predicted by 3-PGN for the five yield classes. All yield classes appeared to be a source of carbon at their establishment with over 2 $\mathrm{tC\,ha^{-1}\,yr^{-1}}$. The first two highest yield classes became a sink at the age

Table 6.1: A summary of some of the major variables of 3-PGN following fitting to the normal yield tables for the five major yield classes. Outputs include above / total biomass ratio, below / total biomass ratio, mean annual gross primary production (P_G, $\mathrm{tC\ ha^{-1}\ yr^{-1}}$), mean annual net primary production (P_N, $\mathrm{tC\ ha^{-1}\ yr^{-1}}$), mean annual autotrophic respiration (R_A, $\mathrm{tC\ ha^{-1}\ yr^{-1}}$), mean annual heterotrophic respiration (R_H, $\mathrm{tC\ ha^{-1}\ yr^{-1}}$), mean annual net ecosystem production (P_E, $\mathrm{tC\ ha^{-1}\ yr^{-1}}$), maximum accumulated net ecosystem production ($P_{E_{AC_X}}$, $\mathrm{tC\ ha^{-1}}$), age at maximum net ecosystem production ($P_{E_{AC_X}\ Age}$), rotation length (years), stand volume at rotation ($V_{\ Rot}$, $\mathrm{m^3\ ha^{-1}}$), stem biomass at rotation ($W_{S\ Rot}$, $\mathrm{tDM\ ha^{-1}}$), foliage biomass at rotation ($W_{F\ Rot}$, $\mathrm{tDM\ ha^{-1}}$), root biomass at rotation ($W_{R\ Rot}$, $\mathrm{tDM\ ha^{-1}}$), stem biomass at maximum net ecosystem productivity ($W_{S\ P_{E_{AC_X}}}$, $\mathrm{tDM\ ha^{-1}}$), foliage biomass at maximum net ecosystem productivity ($W_{F\ P_{E_{AC_X}}}$, $\mathrm{tDM\ ha^{-1}}$), root biomass at maximum net ecosystem productivity ($W_{R\ P_{E_{AC_X}}}$, $\mathrm{tDM\ ha^{-1}}$), age at maximum leaf area index ($L^*_{x\ Age}$, years), maximum leaf area index (L^*_x), mean annual transpiration (R_T, mm), above ground epsilon (ε_{Above}, $\mathrm{gDM\ MJ^{-1}}$), mean annual soil nitrogen availability (N_{AV}, $\mathrm{tN\ ha^{-1}\ yr^{-1}}$) and mean annual tree nitrogen uptake (U_N, $\mathrm{tN\ ha^{-1}\ yr^{-1}}$).

Yield class	Above / Total	Below / Total	P_G	P_N	R_A	R_H	P_E	P_{E_x}	$P_{E_{AC_X}}$	$P_{E_{AC_X}\ Age}$	Rotation	$V_{\ Rot}$
14	0.95	0.05	8.76	4.27	4.49	2.66	1.61	3.85	162.16	91	68	477.39
12	0.94	0.06	8.95	4.36	4.59	2.73	1.63	3.69	164.51	92	71	428.27
10	0.93	0.07	8.77	4.28	4.50	2.69	1.59	3.46	160.14	93	75	379.72
8	0.93	0.07	8.17	3.98	4.19	2.55	1.43	3.20	144.63	92	77	328.61
6	0.91	0.09	7.26	3.54	3.72	2.33	1.21	3.07	122.62	92	82	274.60
4	0.91	0.09	6.26	3.05	3.21	2.10	0.95	2.88	95.69	93	90	208.13

Yield class	$W_{S\ Rot}$	$W_{F\ Rot}$	$W_{R\ Rot}$	$W_{S\ P_{E_{AC_X}}}$	$W_{F\ P_{E_{AC_X}}}$	$W_{R\ P_{E_{AC_X}}}$	$L^*_{x\ Age}$	L^*_x	R_T	ε_{Above}	N_{AV}	U_N
14	205.84	4.84	4.23	251.82	1.96	1.59	24	3.49	329.01	0.20	0.28	1.11
12	184.60	4.69	4.17	222.33	2.03	1.67	24	3.39	324.17	0.20	0.16	1.12
10	163.60	4.26	3.74	191.22	2.01	1.64	24	3.26	291.49	0.20	0.11	1.11
8	141.56	3.97	3.41	158.51	2.07	1.67	29	3.14	292.11	0.18	0.09	1.05
6	118.26	3.28	2.71	128.00	2.06	1.62	34	2.86	275.04	0.16	0.06	0.95
4	89.60	2.41	1.90	93.37	2.11	1.63	34	2.20	223.00	0.15	0.03	0.86

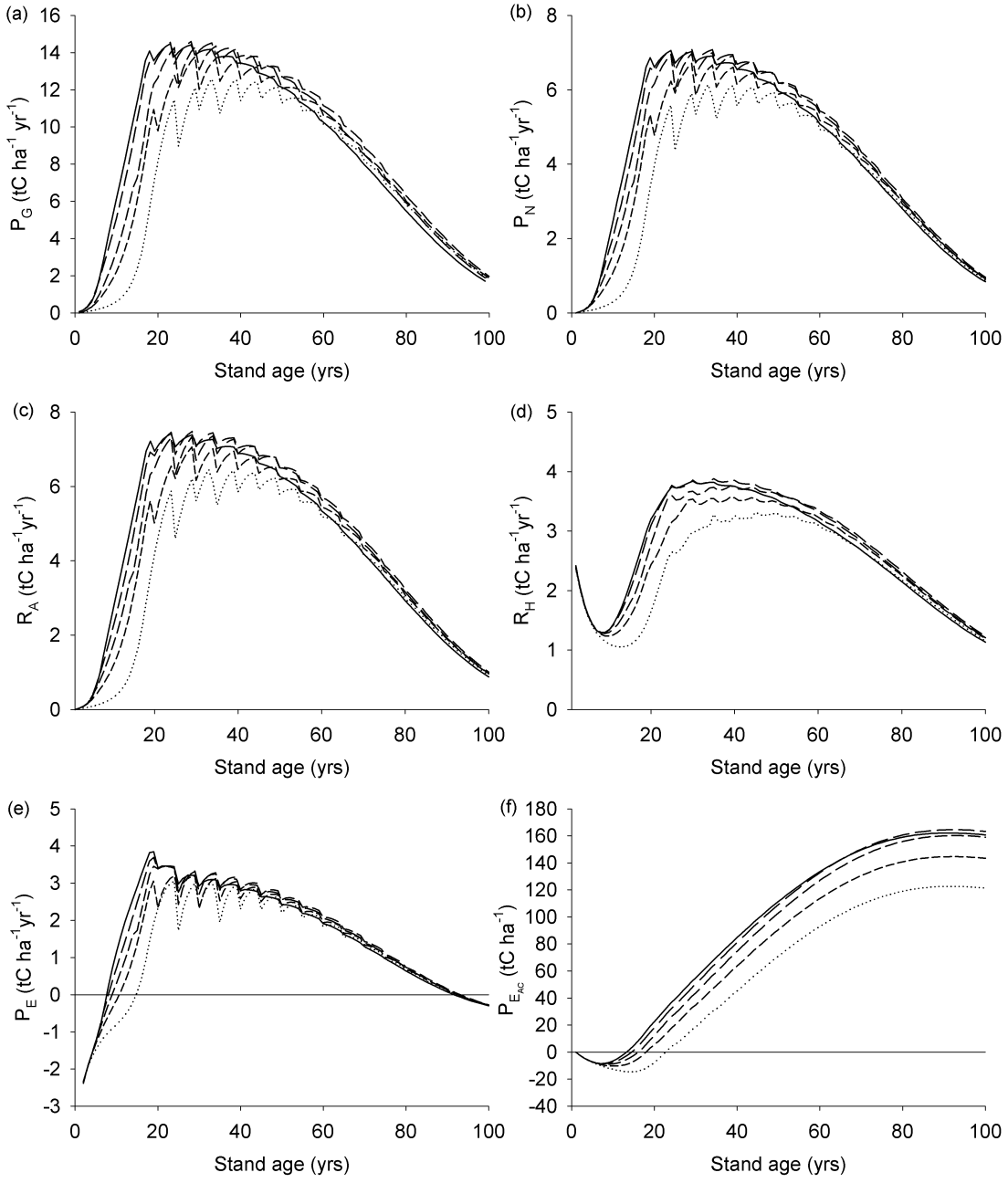

Figure 6.3: Patterns of (a) gross primary production (P_G, $\mathrm{tC\ ha^{-1}\ yr^{-1}}$), (b) net primary production (P_N, $\mathrm{tC\,ha^{-1}\,yr^{-1}}$), (c) autotrophic respiration (R_A, $\mathrm{tC\,ha^{-1}\,yr^{-1}}$), (d) heterotrophic respiration (R_H, $\mathrm{tC\ ha^{-1}\ yr^{-1}}$), (e) net ecosystem production (P_E, $\mathrm{tC\ ha^{-1}\ yr^{-1}}$) and (f) accumulated net ecosystem production ($P_{E_{AC}}$, $\mathrm{tC\ ha^{-1}}$), as modelled by 3-PGN over a 100 year period for yield classes 14 (solid line), 12 (long dashed line), 10 (medium dashed line), 8 (short dashed line), and 6 (dotted line).

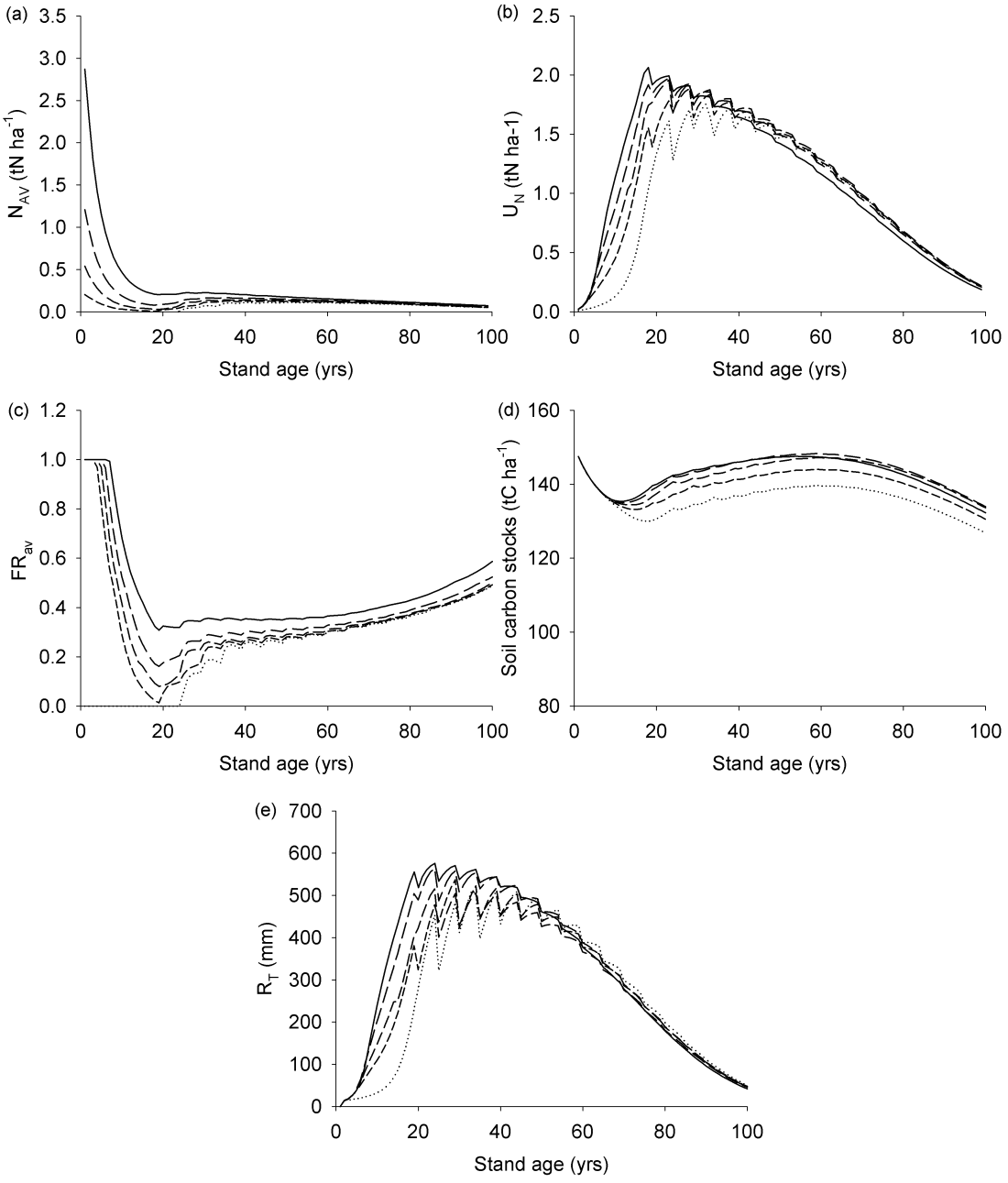

Figure 6.4: Patterns of (a) soil nitrogen availability (N_{AV}, $\mathrm{tN\ ha^{-1}}$), (b) soil nitrogen uptake (U_N, $\mathrm{tN\ ha^{-1}}$), (c) mean annual fertility rating (FR_{av}), (d) annual soil carbon stocks ($\mathrm{tC\ ha^{-1}}$), and (e) annual transpiration (R_T, mm), as it was modelled by 3-PGN over a 100 year period for yield classes 14 (solid line), 12 (long dashed line), 10 (medium dashed line), 8 (short dashed line) and 6 (dotted line).

of eight, while yield class 10 a year after. Yield class 8 became a sink at the age of 11 whereas the last two classes both became a source at the age of 15. The model also showed that all yield classes started to become sources again after 92 years from establishment. Annual P_E over the simulation period peaked at the age of 19 for yield class 14, 12 and 10 with 3.85, 3.69 and 3.46 $\mathrm{tC\ ha^{-1}\ yr^{-1}}$ respectively, whereas for classes 8 and 6 it peaked at the age of 24 and 33 with 3.20 and 3.07 $\mathrm{tC\ ha^{-1}\ yr^{-1}}$ respectively.

Something else to be noticed is that the model predicted a 2 to 9% decrease in soil carbon stocks at the end of the rotation for yield classes 10 to 6, whereas it showed virtually no change for yield class 12 shows an increase of an insignificant 1% for yield class 14. By the time of maximum accumulated net ecosystem production, the soil has become a significant source of carbon with a decrease in stocks from 5% up to 10% (Figure 6.4d).

6.3.2 Biomass, leaf area and timber production

Maximum leaf area index (L_x^*) ranged between 2.2 and 3.5 $\mathrm{m^2\ m^{-2}}$, with maximum L^* occurring between 24 and 34 years after establishment (Figure 6.5e). In terms of timber production, the optimal rotation length for yield class 14 was around 68 years and around 90 years for yield class 4. The stand volume at rotation varied between 208.13 and 477.39 $\mathrm{m^3\ ha^{-1}}$ for yield classes 14 and 4 respectively. Furthermore, mean aboveground epsilon (ε_{Above}) for the 100 years of productivity varied between 0.15 and 0.20 $\mathrm{gDM\ MJ^{-1}\ yr^{-1}}$ (Figure 6.5f).

Figure 6.5b,c and d shows stem, foliage and root biomass across rotation and yield classes. Differences between classes for stem biomass could not be seen for the first ten years from the establishment of the stands, with differences started to appear after that (Figure 6.5b). Foliage biomass appeared to be significantly lower for yield class 6 approximately for the first 17 years from establishment (Figure 6.5c) with similar patterns for root biomass development (Figure 6.5d). A sudden foliage expansion appears around the age of 18.

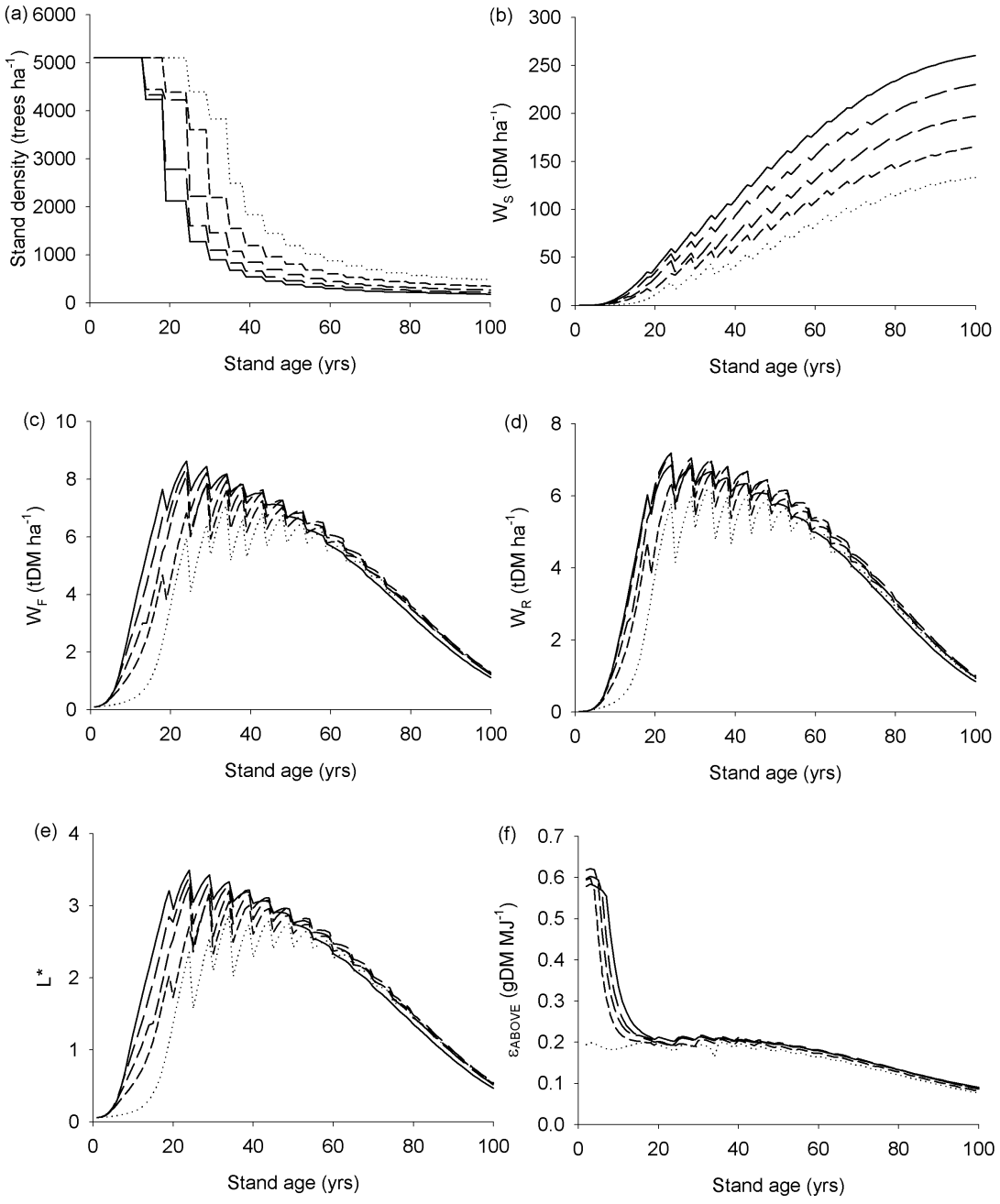

Figure 6.5: Patterns of (a) Stand density ($\mathrm{trees\,ha^{-1}}$), (b) stem biomass (W_S, $\mathrm{tDM\ ha^{-1}}$), (c) foliage biomass (W_F, $\mathrm{tDM\ ha^{-1}}$), (d) root biomass (W_R, $\mathrm{tDM\ ha^{-1}}$), (e) leaf area index (L^*) and (f) above ground epsilon (ε_{Above}, $\mathrm{gDM\ MJ^{-1}}$), as it was modelled by 3-PGN over a 100 year period for yield classes 14 (solid line), 12 (long dashed line), 10 (medium dashed line), 8 (short dashed line) and 6 (dotted line).

Finally the ratio of belowground to aboveground biomass ranges from 0.06 to 0.11, the ratio of belowground to total biomass ranges from 0.05 to 0.09 and the ratio of aboveground to total biomass ranges from 0.95 to 0.91 from the higher yield class to the lower, respectively.

6.3.3 Deviation from normal production due to site conditions

For the seven sites which previously were classified as yield class 14, the new estimated yield class after running 3-PGN varied from 6 to 13 $\mathrm{m^3\,ha^{-1}\,yr^{-1}}$. Rotation length ranged from 68 to 76 years from planting and stand volume at rotation ranged between 330.21 and 445.60 $\mathrm{m^3\,ha^{-1}}$. Maximum $P_{E_{AC}}$ took values from 121.05 to 187.34 $\mathrm{tC\,ha^{-1}}$, whereas this maximum value was achieved between years 87 and 94 after establishment. Similarly, for the sixteen yield class 12 sites, the yield predicted by the model varied from 7 to 13 $\mathrm{m^3\,ha^{-1}\,yr^{-1}}$ with the rotation length between 68 and 84 years and stand volume between 71 and 506.91 $\mathrm{m^3\,ha^{-1}}$. $P_{E_{AC_X}}$ was between 93.76 and 228.88 $\mathrm{tC\,ha^{-1}\,yr^{-1}}$ with these values reached between 84 and 99 years. On the other hand, there were eight sites in class 10 for which the model predicted a yield class between 5 and 9 $\mathrm{m^3\,ha^{-1}\,yr^{-1}}$, whereas the rotation length was between 73 and 85 years and a stand volume between 227.09 and 340.65 $\mathrm{m^3\,ha^{-1}}$. Maximum accumulated net ecosystem is achieved between 86 and 93 years with values ranging between 106.56 and 175.49 $\mathrm{tC\,ha^{-1}}$.

Class 8 had also eight sites with a predicted yield class from 3 to 7 $\mathrm{m^3\,ha^{-1}\,yr^{-1}}$, a rotation length from 77 to 100 years and stand volume at rotation from 200 to 295.37 $\mathrm{m^3\,ha^{-1}}$. $P_{E_{AC_X}}$ was achieved between age 85 and 94 years with values from 96.44 to 156.92 $\mathrm{tC\,ha^{-1}}$. Finally, class 6 has only six sites and their estimated yield class ranged only between 4 and 5 $\mathrm{m^3\,ha^{-1}\,yr^{-1}}$ with rotation length from 82 to 92 years and volume between 181.88 and 244.55 $\mathrm{m^3\,ha^{-1}}$. Maximum accumulated net ecosystem productivity was achieved between year 86 and 93, while values range from 94.79 to 123.17 $\mathrm{tC\,ha^{-1}}$. There were no plots belonging to yield class 4.

Table 6.2 gives deviation from normal conditions for each general yield class. It in-

Table 6.2: Deviation from normality due to site conditions for yield class ($\mathrm{m}^3\ \mathrm{ha}^{-1}\ \mathrm{yr}^{-1}$), maximum accumulated net ecosystem productivity ($P_{E_{AC_X}}$, $\mathrm{tC\,ha}^{-1}$), rotation length (years) and stand volume at the end of the rotation ($V_{\ Rotation}$, $\mathrm{m}^3\ \mathrm{ha}^{-1}$). $\overline{Pred}$ indicates the averaged predicted values for the 45 sites grouped per yield class after running 3-PGN with each site's specific climatic and soil conditions, whereas Dev (expressed in percentage %) gives the deviation from normal conditions.

Yield class			$P_{E_{AC_X}}$			Rotation			$V_{\ Rotation}$		
Normality	$\overline{Pred}$	Dev	Normality	$\overline{Pred}$	Dev	Normality	$\overline{Pred}$	Dev	Normality	$\overline{Pred}$	Dev
14	10	-25%	162.16	148.86	-8%	68	76	12%	477.39	402.97	-8%
12	10	-16%	164.51	156.37	-5%	71	74	4%	428.27	361.42	-5%
10	7	-26%	160.14	147.27	-8%	75	79	5%	379.72	301.87	-8%
8	6	-29%	144.63	126.92	-12%	77	83	8%	328.61	254.08	-12%
6	4	-28%	122.62	106.61	-13%	82	86	5%	274.60	207.60	-13%

cludes 3-PGN results for mean predicted yield class, $P_{E_{AC_X}}$, rotation length and stand volume at rotation (see also Figure 6.6). While normal yield tables suggest that the highest yield class for Scots pine will give a MAI of 14 $\mathrm{m}^3\ \mathrm{ha}^{-1}\ \mathrm{yr}^{-1}$, 3-PGN shown that those sites if the normal thinning is applied in average the predicted increment is reduced to 10 $\mathrm{m}^3\ \mathrm{ha}^{-1}\ \mathrm{yr}^{-1}$, with similar reduction for the second highest productivity class.

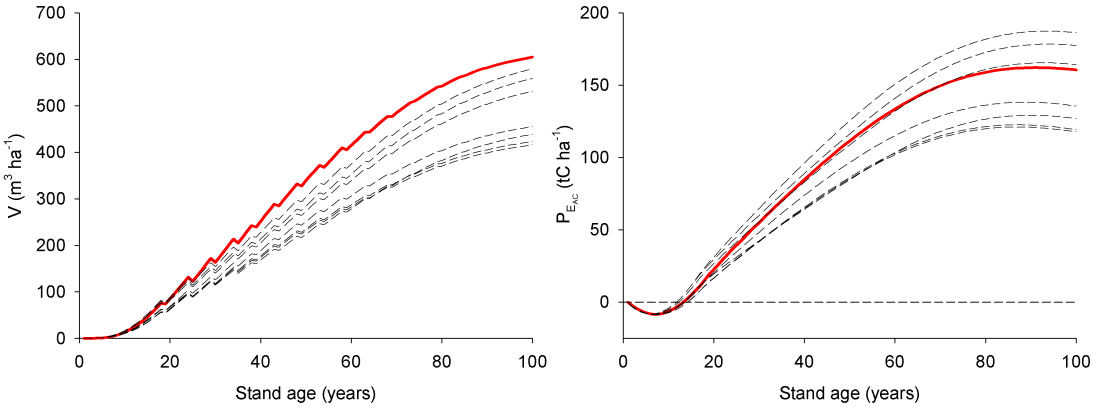

Figure 6.6: Stand volume (V, $\mathrm{m}^3\ \mathrm{ha}^{-1}$) and accumulated net ecosystem production ($P_{E_{AC}}$, $\mathrm{tC\,ha}^{-1}$) deviation from normal conditions for yield class 14. Thick line represents predictions of general yield class.

It is also obvious from Table 6.2 that this reduction in the prediction of yield class is consistent through out the five general yield classes with a reduction of 2 - 4 $\mathrm{m}^3\ \mathrm{ha}^{-1}\ \mathrm{yr}^{-1}$. If we compare the stand volume at the end of the rotation as predicted by the model when fitted to the yield tables and the mean stand volume for each yield class from the

45 sites, we see that generally stand volume is expected to be lower than under normal conditions with the largest difference for the highest productivity classes.

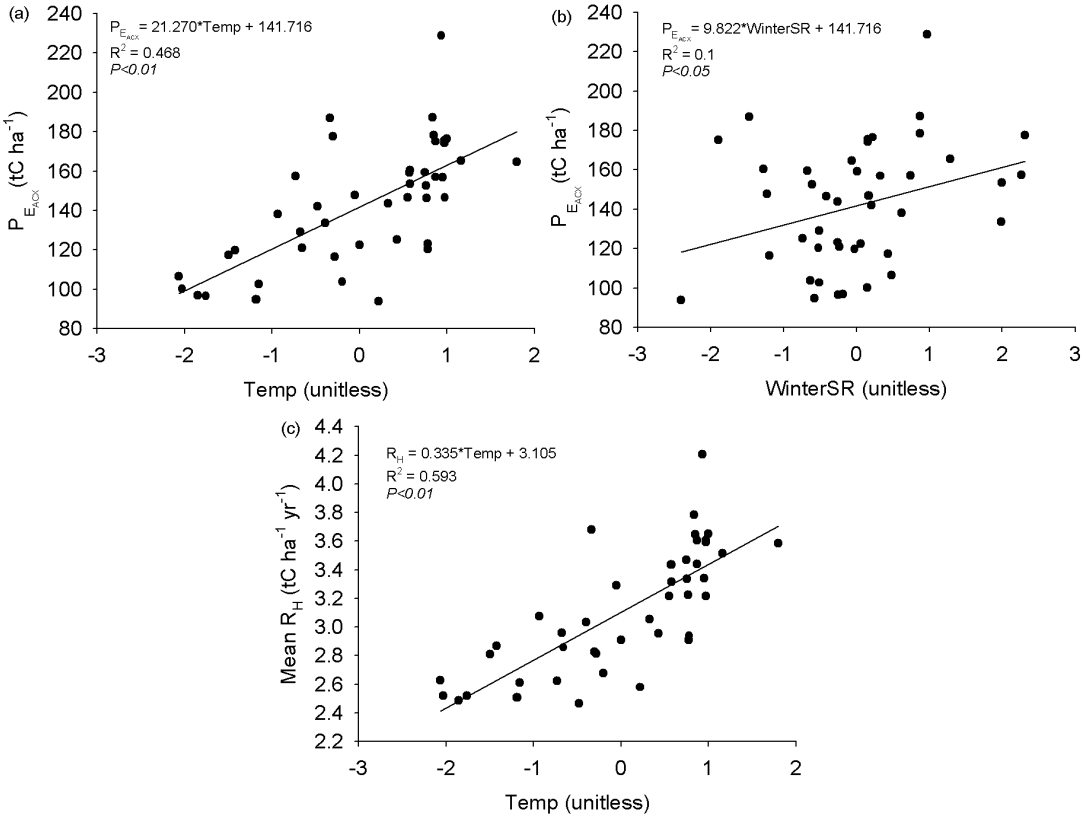

Figure 6.7: Relationships of (a) maximum accumulated net ecosystem production ($P_{E_{AC_X}}$, $\mathrm{tC\ ha^{-1}\ yr^{-1}}$) with component factor for temperature ($Temp$,unitless), (b) component factor for solar radiation ($WinterSR$, unitless) and (c) mean heterotrophic respiration (R_H, $\mathrm{tC\ ha^{-1}\ yr^{-1}}$), with component factor for temperature.

The difference between fitting to the yield table and averaged values in regard to carbon accumulation and fluxes were found to be smaller for high productivity classes. The highest productivity class accumulated about 8% less carbon, whereas the lower class accumulated almost 13% less. Similar effect appeared for the standing volume at the age of the rotation. However, the actual length of the rotation appeared to be longer for the higher productivity stands.

The variation in carbon accumulation and timber production was also explored in relation to environmental factors. Figures 6.7 and 6.8 illustrate some of the relationships with principal component factors (see Chapter 3). Significantly ($P < 0.01$), $P_{E_{AC_X}}$ was positively related with the principal component factor for temperature ($Temp$),

whereas a weaker relationship exists with winter solar radiation ($WinterSR$). Also highly important is the relationship between mean heterotrophic respiration component factor for temperature. On the other hand, predicted volume increment is significantly related with both component factors for temperature and winter solar radiation. Finally, of great interest appear to be the relation between nitrogen availability and the factor for lack of precipitation and nitrogen uptake with the temperature component factor (Figure 6.8).

6.3.4 Timber and carbon productivity classes

Figures 6.9 and 6.10 present classes derived after the simulations for the 45 sites for V, L^*, MAI, CAI, FR_{av}, N_{AV}, U_N and $P_{E_{AC_X}}$. Also, Figure 6.11 compares the resulting classes with those from the yield tables. Only five classes are presented as they were

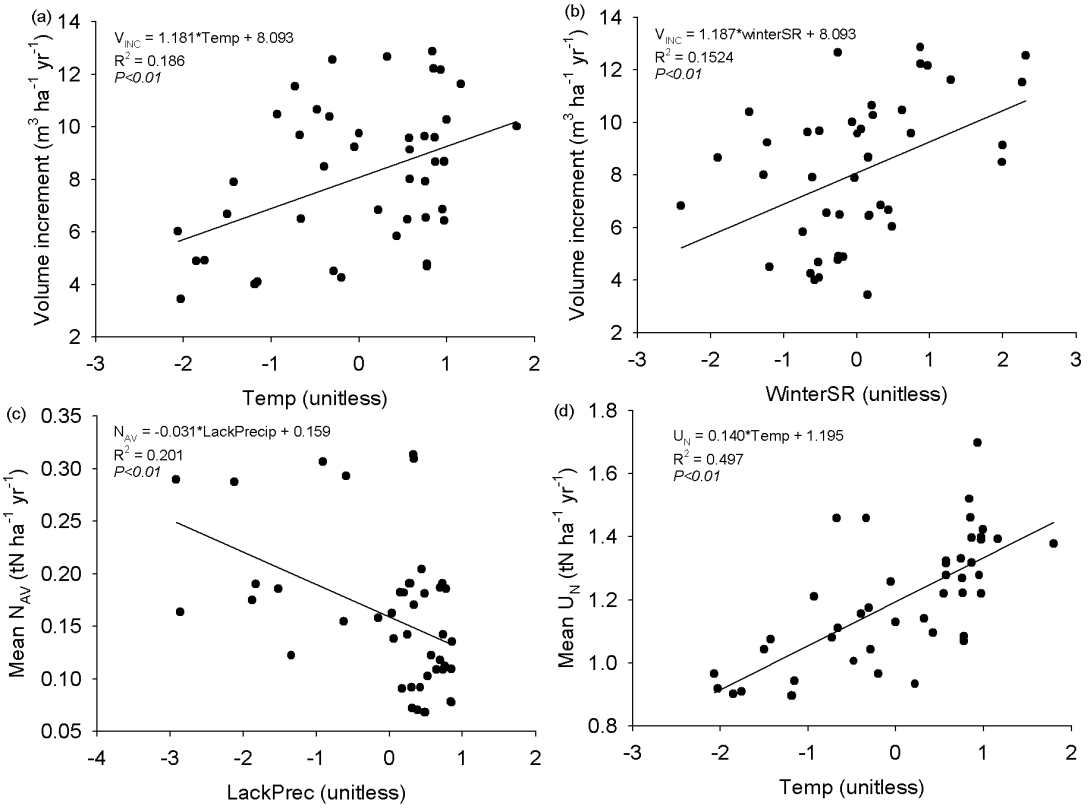

Figure 6.8: Relationships of volume increment ($\mathrm{m}^3\ \mathrm{ha}^{-1}\ \mathrm{yr}^{-1}$) with (a) principal component factor for temperature ($Temp$, unitless), (b) winter solar radiation ($WinterSR$, unitless) and mean annual soil nitrogen availability (N_{AV}, $\mathrm{tN\ ha}^{-1}\ \mathrm{yr}^{-1}$) with (c) component factor for lack of precipitation ($LackPrec$, unitless)and (d) mean nitrogen uptake (U_N, $\mathrm{tN\ ha}^{-1}\ \mathrm{yr}^{-1}$) with temperature factor.

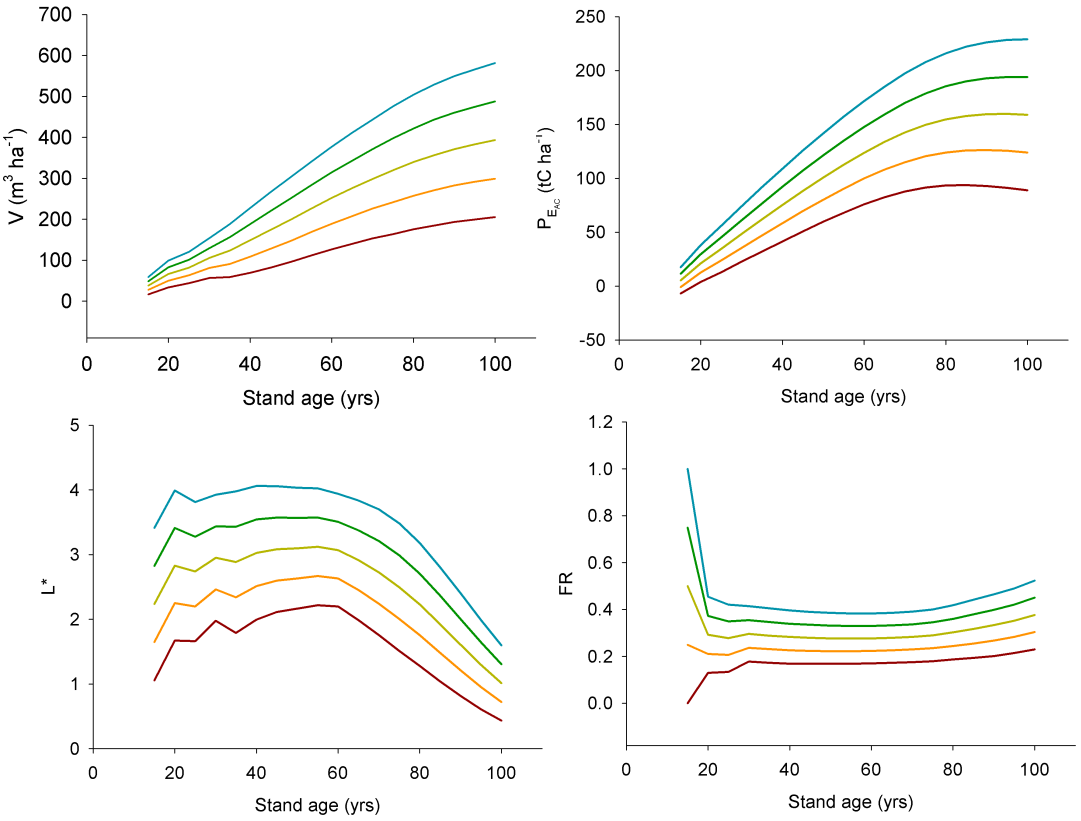

Figure 6.9: An example of several 3-PGN's variables classes as they were produced from application of the model for 45 Scots pine stands. Stand volume (V, $\mathrm{m}^3\ \mathrm{ha}^{-1}$) , leaf area ($L^*$), accumulated net ecosystem productivity ($P_{E_{AC}}$, $\mathrm{tC\ ha}^{-1}$) and site fertility are some of the outputs which classes were produce as a demonstration of the possibilities a simplified ecosystem model such as 3-PGN offers for alternative site classification.

no sample plots belonging to the lowest class. A better look at volume curves showed that the yield tables tented to underestimate values for the lowest classes during the first few decades of the stand's life. On the other hand, yield tables appeared to be optimistic in comparison to model results, at the end of the rotation. This difference was translated into longer rotations from those given by yield tables (Table 6.2).

6.4 Discussion

6.4.1 Model restriction by normal yield tables

One of the objectives of the study was to constrain 3-PGN's predictions according to the yield forecast by normal yield tables. This was achieved by introducing different

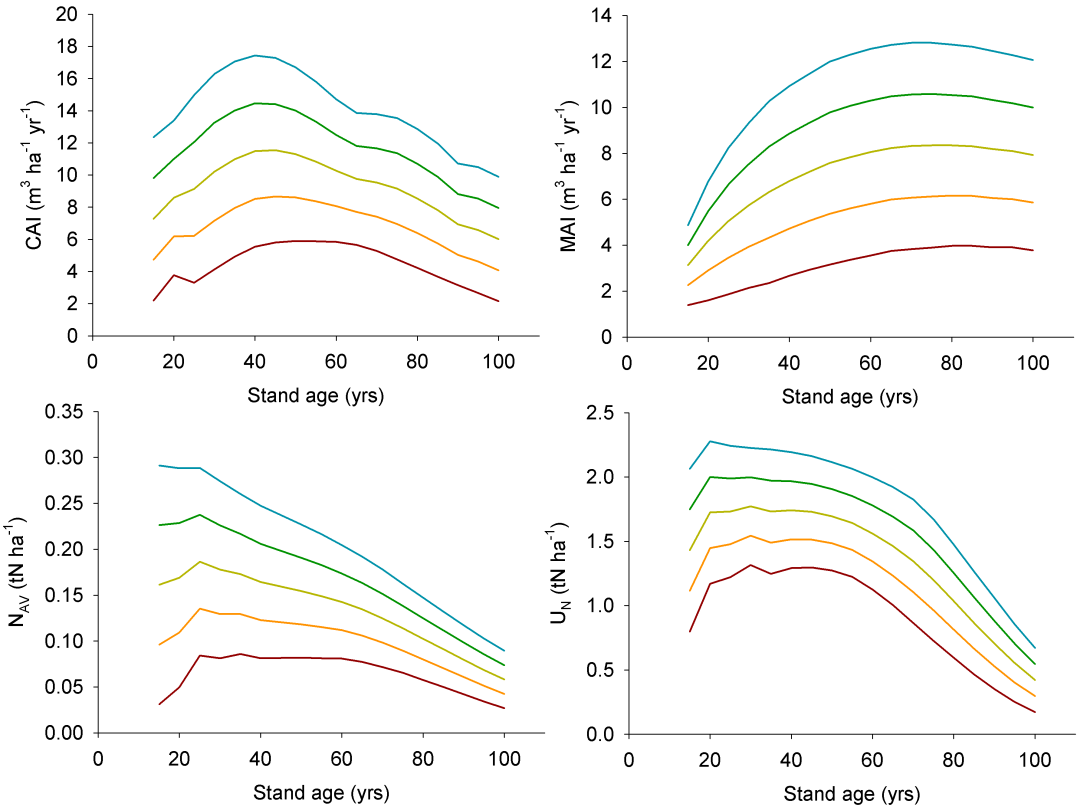

Figure 6.10: Site classification could be succeeded not only through estimation of the current annual (CAI, $\mathrm{m}^3\,\mathrm{ha}^{-1}\,\mathrm{yr}^{-1}$) or mean annual ($MAI$, $\mathrm{m}^3\,\mathrm{ha}^{-1}\,\mathrm{yr}^{-1}$) increment but also by estimating soil nitrogen availability (N_{AV}, $\mathrm{tN\,ha}^{-1}$) and tree nitrogen uptake (U_N, $\mathrm{tN\,ha}^{-1}$). For such alternative site classification to be applicable a thorough investigation of all current soil nutritional status of the species under investigation should be included.

environmental and nutritional conditions. The important step was to derive a thinning regime capable of coping with such restriction. The thinning regimes for the higher productivity classes the first few years thinning removal was negligible, with an increase to around 40% removal of the mean tree by the age of 25. By the end of the 100 years roation thinning is reduced to minimum (aproximately 2% of the mean tree biomass). Similar patterns were also observed for yield class 12 (Figure 6.1). However, as yield class was reduced, thinning had to start from very high percentages indicating the need for thinning from above, where amongst the trees removed, healty trees are also included.

Our strategy for fitting yield tables was based on the assumption that the applied thinning follows the stocking suggested by the tables. It could be the case however, that if timing and number of trees after thinning were different, there would not be a need for

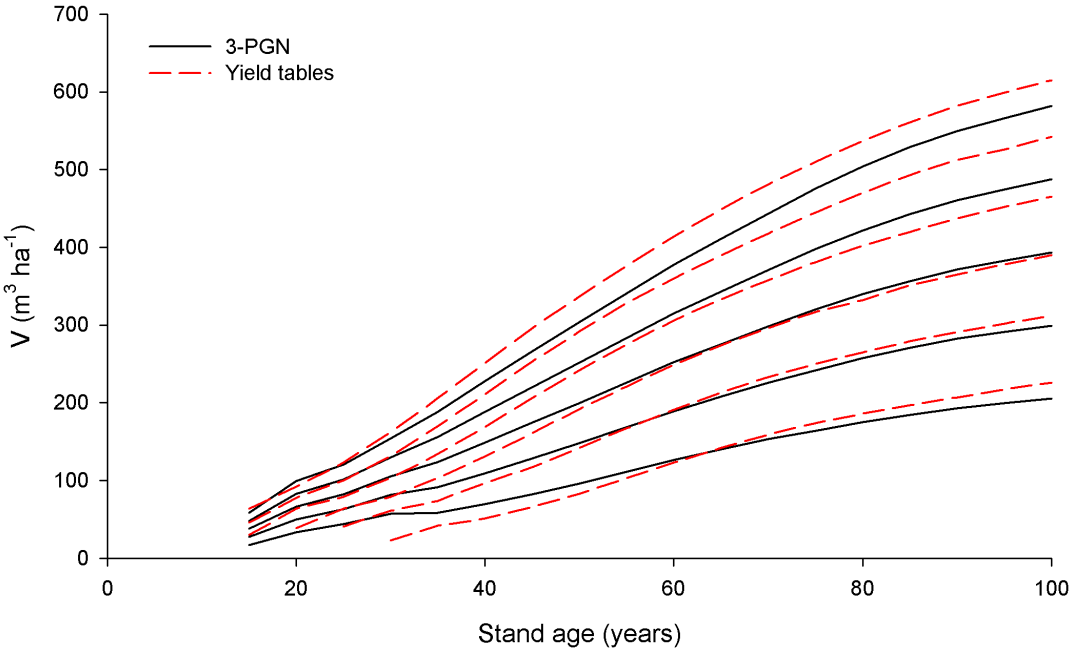

Figure 6.11: Comparison between modelled volume classes produced from sample plots (solid lines) versus volume classes as given by normal yield tables (long dashed lines). Model and yield tables do not differ significantly at the beginning of stand's development. This changes to a slight overestimation by yield tables at the end of the 100 years period. However, for the low productivity there is a significant difference between model and yield tables. Model overestimated in comparison to the yield tables, whereas the opposite happened as stand grow older.

such extreme thinning regimes. 3-PGN clearly found it very difficult to match patterns for lower productivity sites. Additionally, 3-PGN was unable to match perfectly the lowest yield class 4 patterns, especially at the early stages of the stand's development (Figure 6.2). Extreme thinning and nutrient limitation were also necessary to be able to fit yield table values only after the first thinning. This inability of the model to fit low productivity classes could also be seen in Figure 6.11, which shows the effect that site and environmental conditions have on normal production. 3-PGN produced more at the beginning of a stand's life, while it very singificantly reduces productivity much later. Which is the factor responsible for those difference it is unkown. But as results in Chapters 3 and 5 have shown, winter temperatures and soil drought can significantly limit Scots pine growth, which could explain this difference.

6.4.2 Leaf, biomass and timber development

Similar observations can be made for stem biomass development. Highly productive stand produce stem biomass rapidly within the first twenty years from the establishment of the stands (Figure 6.5). The rate of foliage biomass development is more rapid for higher productivity classes (Figure 6.5c), whereas the rates of root biomass are not significantly different except for yield class 6 (Figure 6.5d). The model also showed that leaf area index in high productivity stands increased with a rapid rate, reaching maximum values much earlier than at low productivity sites. The differences in nutrients increased growth rates causing rapid leaf development (Figure 6.5e). Differences between yield classes exists up to 60 years from establishment. After the age of 60 values were not significantly different any longer. Combined with the fact that differences in stem biomass were not large before the age of 25, this suggests that, as stands grow older, allocation to roots and foliage becomes similar with the main differences in stem production. The similarities in root biomass must be due to the equilibrium in nitrogen mineralisation caused by a similar equilibrium in litterfall rate. This equilibrium litterfall rate reduces foliage biomass as stands grow older. Thus, foliage biomass is predicted to be identical for all yield classes, because of equal litterfall rates and consequently litterfall, as the model lacks any environmental effect on litterfall rates.

When 3-PGN was run for a single site with a constant specific leaf area of 6 $\mathrm{m}^2\ \mathrm{kg}^{-1}$ and a litterfall rate 0.02083 per month (assuming that needles are retained for 4 years) then the estimation of foliage biomass was on average almost 48% higher than the current time-dependent specific leaf area and litterfall rate. In a similar way, giving a constant specific leaf area increased foliage biomass by a mean of 30%, while applying a constant littefall rate produced in average 19% more foliage. Nevertheless, predicted L^* values (1.94 ± 0.06) come in good agreement with observations by Mencuccini and Bonosi (2001), who gave a value of 2.0 for Scots pine at the age of 70. Finally, the model showed that the ratio of above ground biomass to total biomass decreased when productivity was reduced, while the ratio of belowground to total biomass is increased. This suggests that low production stands allocate more to roots than to stem or foliage, which could be due to large competition for nutrients.

6.4.3 Carbon and nitrogen fluxes under normality

Many studies have explored net primary production of Scots pine across the boreal region (Schulze *et al*., 1999; Gower *et al*., 2001), or the effect of drought and phenology on production across a geographical gradient (Berninger, 1997), while others have illustrated production of Scots pine in a chronosequence managed by clearcutting (Kolari *et al*., 2004) and periodically disturbed by fire (Wirth *et al*., 2002). However, only a few studies have investigated carbon sequestration under current management (Cannell and Milne, 1995; Waring and McDowell, 2002).

Working in a chronosequence of Scots pine, Kolari *et al*. (2004) found that stands were source of carbon up to 12 years old, where P_E became zero. This matches 3-PGN results, for the highest productivity stands, which were source of carbon for up to 8 years, whereas the lower productivity stands up to 15 years. For 4 year old stands, P_E was -2.62 $\mathrm{tC\,ha^{-1}\,yr^{-1}}$ which comes in very close agreements with the value of -2.39 $\mathrm{tC\,ha^{-1}\,yr^{-1}}$ predicted by 3-PGN. The model also produced reasonable results for 40 year old stands, with Kolari *et al*. (2004) giving values of 2.42 $\mathrm{tC\,ha^{-1}\,yr^{-1}}$, while 3-PGN estimates P_E from 2.3 to 2.8 $\mathrm{tCha^{-1}yr^{-1}}$. However, the model showed a decrease in productivity for the older stands of the age of 75 with 1.3 $\mathrm{tC\,ha^{-1}\,yr^{-1}}$, while Kolari *et al*. (2004) reported an increase to 2.53 $\mathrm{tC\,ha^{-1}\,yr^{-1}}$. The model appeared to reduce productivity for all yield classes, which was either due to extreme effect of the age modifier or because of the fast reduction of foliage biomass.

Cannell and Milne (1995) in a national study for Great Britain showed that Scots pine had a potential carbon storage of 178 $\mathrm{tC\,ha^{-1}}$ for a yield class 10, which is slightly higher from our prediction of 160 $\mathrm{tC\,ha^{-1}}$. Rotation on the other hand, for the same stand was predicted at 71 years, which comes in close agreement with our prediction of 79 years.

As expected, high productivity stands became carbon sinks much earlier than low productivity stands with values up to 4 $\mathrm{tC\,ha^{-1}\,yr^{-1}}$. However, we observed again that, after a certain age (approximately 60 years) net ecosystem production became very similar, with all stands becoming a source of carbon again around the age of 90. Accu-

mulated net ecosystem productivity provided an adequate indication of an ecosystem's capability for carbon sequestration. Table 6.1 showed that highly productive stands did sequester more carbon from the lower productivity classes. However, the age at which this is achieved did not appear to be significantly different (approximately 92 years). Interesting again is the fact that non-significant differences existed between the two lowest productivity classes, which suggests that the main difference between them is mainly in stem development. Nevertheless, we must not forget that information about growth of yield class 6 before the age of 25 were not available.

Fertility rating on the other hand, showed great differences between classes for the first 40 years, with differences also in initial values due to differences in initial mineralisation rates. The rate of change in fertility rating should be the key indication for the nutritional status of each yield class. High productivity stands appeared to have a slower decrease in fertility, whereas lower yield classes appeared to have a sharper decrease. The different rates of decrease between classes shows that more productive stands have an excess of nitrogen which they utilize slowly, while lower productivity classes have less mineralised nitrogen and the utilization becomes much faster. However, as the stand grows older, nutrient supply from litterfall reaches an equilibrium demand from foliage with the biomass production have given different values for fertility across yield classes.

6.4.4 Effect of site condition on carbon sequestration and timber production

When 3-PGN was run for the 45 sites following the fitted thinning regime corresponding to each stand's yield class with also the corresponding soil and climatic conditions for each site, a comparison between the summarized results per yield class and the yield tables showed that site conditions have a quite significant effect on yield, reducing timber production by approximately 30% (Table 6.2). The highest deviation from normal conditions appeared for the lower yield classes, suggesting that the limitation of temperature and soil drought, know to effect Scots pine growth (Chapter 3), is greater. Such stands are most likely to grow on well drained, low nutrient soils, which ampli-

fies the drought during the late spring, early summer months where rainfall reaches its minimum (see also Figure 3.8 in Chapter 3). The model also showed the createst impact on highly productive stands where it was found they produced about 25% less timber and taking 12% longer to reach maximum increment.

On the other hand, carbon sequestration of high productivity stands did not appear to be affected hugely by site conditions, as maximum accumulated ecosystem production was reduced by only 8%. However, the same does not apply for low productivity stands, which appeared to accumulate about 13% less carbon from what yield tables have predicted. A very likely explaination for this could again be soil drought stress, which has a great effect on soil respiration. Yuste *et al*. (2003) found that soil respiration for a Scots pine maritime forest in Belgium, growing on poorly drained soil, was mainly controlled by temperature. During late spring - early summer where rainfall was limited, soil water availability and respiration was reduced, but also with respiration becoming more insensitive to temperature. However, when a rain event occured it appeared to stimulate soil respiration with temperature becoming once again the main controling variable. It is likely that such a phenomenon could be enhanced for well drained soils and that, together with the restrictions on photosynthesis due to lack of water, would explain why low productivity stands are capable to accumulate less carbon. Alhtough our data do not appear to support such an argument (Figure 6.7d) their are not enough either to completely dismissed it.

When model estimates for the 45 sites were plotted versus principal component factors derived from climatic and topographic variables, $P_{E_{AC_X}}$ showed a strong positive relation with the factor for temperature (Figure 6.7a). A detailed explanation of the factors can be found in Chapter 3. It appears that sites situated in low elevation accumulated more carbon because of the higher nitrogen uptake (Zianis and Mencuccini, 2005). Photosynthetic activity was also found to be significant during winter months (Chapter 3). When maximum accumulated ecosystem production was plotted with the factor for winter incoming solar radiation a not so strong relation was found. Nevertheless, the existing trend shows northern stands accumulating less carbon. On the other hand, volume increment was found to have slightly stronger relationship with winter radiation

(Figure 6.8b) supporting the findings in Chapter 3.

The high carbon sequestration of low elevation stands was found to be due to two main reasons. Firstly, because of low heterotrophic respiration as Figure 6.7c shows and secondly because of high nitrogen uptake (Figure 6.8d). Additionally, the relation with $Temp$ shows heterotrophic respiration to be higher for more fertile sites something supported also by Zerva *et al*. (2005).

Finally, the relationship between nitrogen availability and the factor for spring-summer drought (Figure 6.8c) agrees with the findings in Chapter 3 showing drought stress as during this period decomposition is restricted, reducing significantly nitrogen mineralization, thus growth.

6.4.5 Productivity classes based on physiological principles

The comparison between normal yield class and the classes produced by 3-PGN (Figure 6.11) showed a differences, which as discussed previously it is most likely to be due to effect of site conditions that the model was able to capture. However, other possible explanations should also be considered, including the observed difference being a considerable effect of the age modifier used in 3-PGN to account for the age-related decline in productivity (Landsberg and Waring, 1997; Magnani *et al*., 2000). During calibration procedures parameters used for estimating the age modifier were not included into the calibration parameter set, but they where chosen to match observed patterns (Magnani *et al*., 2000), without values for F_a, n_{age} and $rAge$ been questioned before. A literature review across species, gave a range of values between 80 and 400 for F_a, while $rAge$ was 0.95 for the majority of species. Landsberg *et al*. (2005) used values of F_a = 500 and $rAge$ = 0.95 for Scots pine in Finland, with Patenaude *et al*. (2005) using the same values for Scots pine in the UK. Assuming always the choice of values for the age modifier was correct and that the difference is not due to site conditions, it shows that Scots pine production was overestimated by the tables for the last stages of a stand's life, whereas it was underestimated for the lower productivity stands and for the early stages.

The major concept behind the fitting procedure of 3-PGN to normal yield tables was to obtain a thinning regime for the model constraining productivity in such a way that the results of stand volume, mean annual and current increment matches the patterns of yield tables. In this procedure certain assumptions were necessary such as: 1) the derived parameter set using the Bayesian calibration approach (Chapter 4), described adequately all growing conditions of Scots pine and that parameters are not significantly different between different site conditions, 2) the parameter set was assumed to be able to produce reliable patterns of net gross and primary production and soil fluxes when the fit to yield tables was achieved and 3) that variables responsible for the differences between classes are climate, soil nutrient status and soil water holding capacity (including soil texture), with the latter assumption adopted by running 3-PGN for the ”mean site” of a yield class.

Using results from the application of 3-PGN for the 45 sites across Scotland we were able to develop classes including volume, maximum accumulated ecosystem productivity, leaf area index, fertility rating (Figure 6.9), current and mean annual volume increment, nitrogen availability and tree nitrogen uptake (Figure 6.10). This simple exercise was performed to demonstrate a simple, basic concept of site classification now based on variables other than timber increment. With the procedure followed, we wanted to demonstrate a new way of thinking for constructing tables predicting an array of variables, all valuable to both ecologists and managers for supporting sustainable management in ecosystem level.

The proposed methodology includes the parameterisation of a model such as 3-PGN for a certain species (e.g., Scots pine), using a modern and automated approach such as the Bayesian calibration using data describing wide range of growing conditions. The following step includes running the model for a range of ”construction” plots, with a wide range of soil and climatic conditions and producing prediction for many of the major outputs. When necessary, adjustments in the parameter set or initial state variables should be deployed to match reality. The produced scatter graphs can then be divided into a number of equi-distance bands, describing different production classes.

However, such methodology has certain key points necessary of attention. The first

issues is that the parameter set should be able to represent adequately the growing conditions of the species, using a set of calibration and validation data set. The second issue is the validity of the produced results for the ”construction” plots. Although, extra validation data for those data would be the ideal, such thing is most often difficult. In such a case, a good calibration and validation set will ensure that produced outputs are representative of reality. Despite the large number of field data that might be necessary, the methodology could be applicable, as data from current permanent sample plot network are sufficient. Nevertheless, the advantage of such a procedure is the physiologically based prediction of growth in different climatic and soil conditions and the possibility of new site classification scheme based on ecosystem level.

6.4.6 Carbon vs timber: which option for management?

Nowadays, modern management policies demand a change in the role of forest plantation as a mean for reducing atmospheric carbon concentration. This new role sometime comes in contradicts the most common management options for a plantation, that is of timber production. To decide which option should be the optimum for a certain type of stand's growth potential, an indication of ecosystem capacity for carbon sequestration must be compared with the equivalent dynamics for timber production.

Cannell and Milne (1995) showed that maximum accumulated net ecosystem production does not match the point were current and annual volume increment are equal (rotation time) with $P_{E_{AC}}$ reaching only one third of the maximum value, for a range of conifer and deciduous species in Great Britain. Similarly, they demonstrated that increase in growth rates and yield production of Sitka spruce will significantly increase carbon storage. Finally, they showed that neither rotation nor maximum carbon storage occurs at the time of maximum MAI. However, they argue that harvesting before or after the time of maximum MAI will simply decrease the amount of carbon stored in the forest ecosystem.

In a similar way, we produced results for rotation length, mean and annual increment as well as accumulated net ecosystem production and age at which this becomes max-

Table 6.3: Rotation length (years), age at maximum net ecosystem production ($P_{E_x\ Age}$, yrs), maximum net ecosystem production ($P_{E_{AC_X}}$, $\mathrm{tC\ ha^{-1}}$) and mean annual net ecosystem production at the end of the rotation for each yield class. The last column gives the carbon not sequestered ($\mathrm{tC\ ha^{-1}}$) when a stand is clear felled at the end of the rotation and not at the point when accumulated net ecosystem production is maximized. The smallest loss is for low productivity stands, whereas the highest is for high productivity stands.

Yield class	Rotation	$P_{E_x\ Age}$	P_{E_x}	$P_{E_{AC}\ Rotation}$	Carbon not sequestered
14	68	91	162.16	146.90	15.26
12	71	92	164.51	151.47	13.04
10	75	93	160.15	151.23	8.88
8	77	92	144.63	138.43	6.19
6	82	92	122.62	120.14	2.48
4	90	93	95.69	95.45	0.25

imum for each yield class (Table 6.3). Figure 6.12 shows the rotation age and age of maximum accumulated net ecosystem productivity for yield class 14 and 6. Rotation length for yield class 14 is 68 years, whereas $P_{E_{AC_X}}$ is achieved at the age of 91. As stand's potential for growth decreases, rotation increases at 82 years for yield class 6. However, $P_{E_{AC_X}}$ is achieve at the age of 93. Table 6.3 shows that by extending the year of final felling of lower productivity stands for 10 years, the loss of non-sequestered carbon is only 2 $\mathrm{tCha^{-1}}$. Since lower productivity stands could be potentially not profitable for timber and the cost in non-sequestered carbon is not great, with an extension of the rotation length a vital management option could be carbon sequestration. On the other hand, extending the rotation length for high productivity stands is not profitable because the point of maximum current annual increment is lost, although the gain in carbon is 17 $\mathrm{tC\ ha^{-1}}$.

Similar are the findings by Liski *et al*. (2001), who showed that Scots pine stored larger amounts of carbon when rotation length was longest suggesting that longer rotation lengths should be favourable for carbon sequestration despite the fact that such a strategy will decrease revenues of landowners. Considering however, that soil respiration after clearfelling occurs at a rate of 5.6 ($\pm\,0.4$) $\mathrm{tC\ ha^{-1}\ yr^{-1}}$ (Zerva *et al*., 2005), then with a year gap between clearfelling and re-establishment of trees the actual gain from a 10 year extension of the rotation length goes down to 9.66 $\mathrm{tC\ ha^{-1}}$.

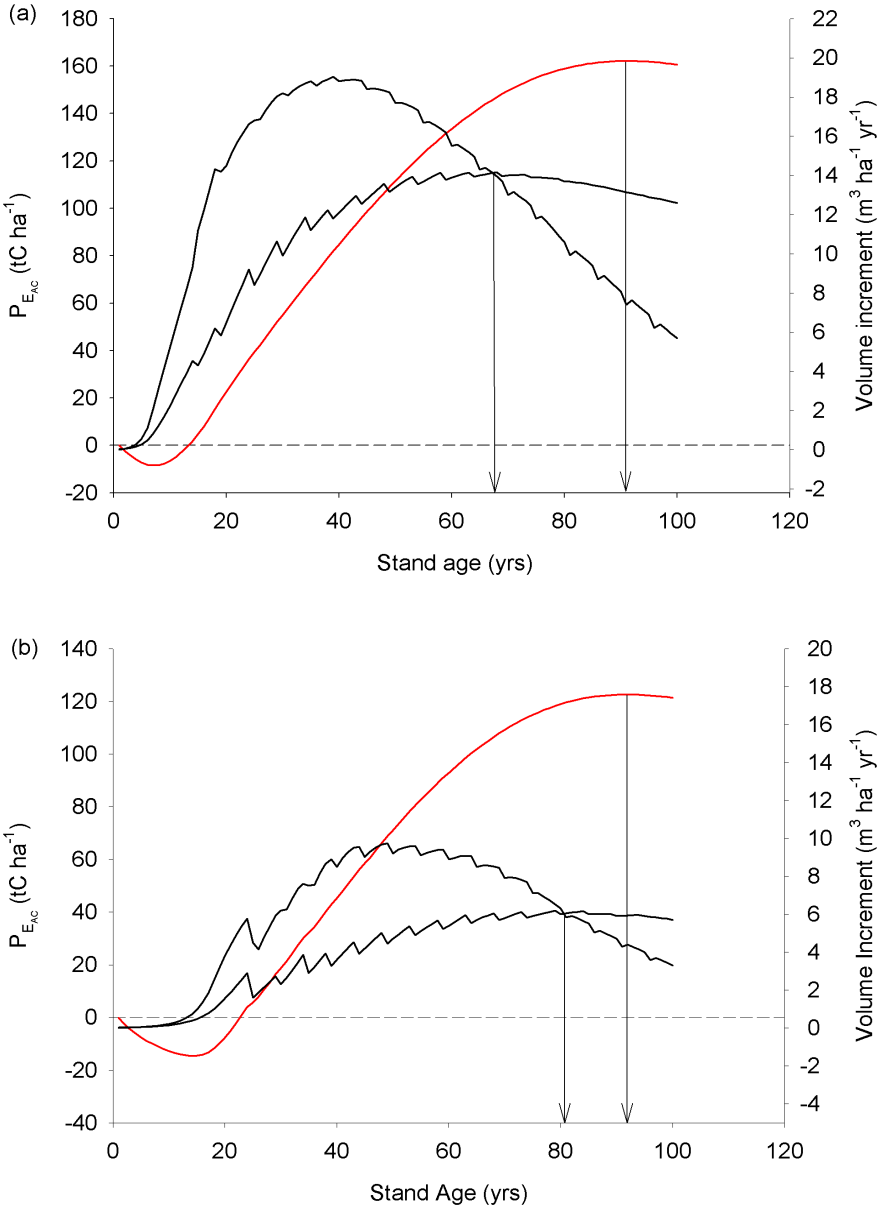

Figure 6.12: Accumulated net ecosystem productivity ($P_{E_{AC}}$), mean annual (MAI) and current annual (CAI) volume increment for (a) yield class 14 and (b) yield class 6. Arrows indicate age at maximum $P_{E_{AC}}$ and rotation age (i.e., age which $MAI = CAI$).

However, in those cases where planting does not take place straight after felling then extending the rotation length for productive stands could be costly both for timber production and carbon sequestration. On the other hand, extending the rotation length for low productivity stands, clearfelling them and re-planting within one year will cause a loss of carbon from the ecosystem of about 3.12 $\mathrm{tC\ ha^{-1}}$. However, because such stands are not expected to have a large contribution in timber production, management

of those stands could concentrate only in carbon sequestration, assuming that no clear-felling takes place. Such stands should also be suitable for conversion into a continuous cover management systems, with the potential to enhance productivity, carbon accumulation and provide a steady source of timber fulfilling in the same time the need for a steady terrestrial carbon sink.

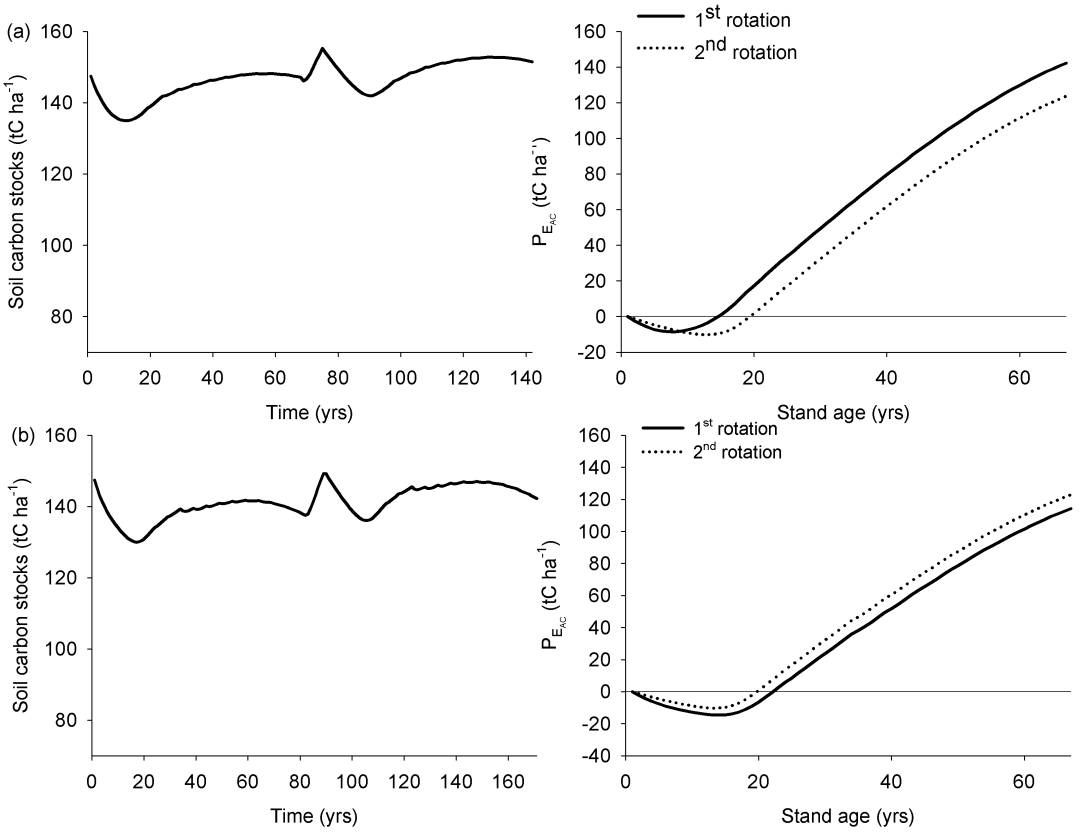

Figure 6.13: Modelled soil carbon stocks ($\mathrm{tC\,ha^{-1}}$) and accumulated net ecosystem production ($P_{E_{AC}}$, $\mathrm{tC\ ha^{-1}}$) for two rotation lengths of (a) a yield class 12 site and (b) a yield class 6 sites. An interval of 7 years was assumed between the two rotations in which soil decomposition was assumed to continue with similar rates as under forest cover, while inputs were assumed only from dead roots with a constant turnover rate of the root biomass existed at the end of the rotation. As a result of the second rotation, a high class site will cause an increase in soil carbon stocks, however its capacity for carbon storage is significantly reduced on the second rotation. Furthermore, the second rotation stand need a few years more to become a carbon sink than the first rotation stand. On the other hand, the lower class stand appears to have a reduction in soil carbon stocks. Interestingly, the capacity for carbon storage is increased as a results of the continues soil nutrient build up, which suggest that low production, second rotation stands will be more productive.

Nevertheless, many questions arise from such a management decision like what are the respiratory losses of an uneven-aged structured forest during and after timber extraction operations, how much carbon is removed during yield removal operations and which silvicultural system is more vital for achieving carbon sequestration.

Other question concerning plantations, is what is the carbon sequestration potentials of second rotation stand. It is known that second rotation has a positive effect on carbon accumulation in the soil (Zerva, 2005), however it is unknown what is the respiratory losses after the clearfelling of the second rotation and if stands continue to be sinks at a third rotation.

A quick investigation into the effect of a second rotation on different productivity stands using 3-PGN showed that for high productivity stands soil carbon stocks increased after the end of the second rotation, while the capability for carbon storage decreased during the second rotation (Figure 6.13). On the other hand, lower productivity stand although appeared to have lower carbon stocks the actual capability for carbon accumulation increased. However, no field data are available to support such a theory and thus further investigation is necessary into the effect of several rotations on different productivity stands on ecosystem carbon dynamics.

6.5 Conclusions

3-PGN belongs in the family of models, where with simplified illustration of the major physiological processes of forest growth, provides adequate information relevant to managers and ecologists. This advantage makes it very useful tool for providing answers to questions arising by the new role of forests as an atmospheric carbon sink.

Two were the main questions of this study. First we wanted to know how much carbon is sequestered when stands follow normal production and second what was the combined effect of site conditions and current management on carbon sequestration. Our results showed that following existing thinning procedures there is a significant lost in timber production, but not large in terms of carbon sequestration. On the other hand, new questions arising, such as what are those silvicultural treatments that can maximize both timber productions and carbons sequestration.

We also found that to maximize carbon sequestration extending the rotation length by a minimum of 10 years for high productivity stands would be an option, with of

course the expected financial implications. However, there is a possibility to ensure a stable carbon sink in a forest ecosystem by retaining low productivity stands since their viability in the timber market is low, and change their silvicultural treatment from a clearfelling to a continuous cover forestry. In this way, we ensure maximizing the value of forest, both in terms of carbon and timber as there is a continuous source of timber supply and a lasting carbon sink, with recreational activities also increasing their real value. Of course other questions, such as how much carbon is actually retained in a continuous cover forest and what are the respiratory losses when productivity becomes low or how much carbon is lost from removals and respiration losses cause by thinning are amongst the important need to be considered beforehand.

Finally, we discussed the application of a new methodology for producing tables including variables meaningful to eco-physiologists, ecologists and forest managers. We recognise the fact that such a procedure could be data demanding, however the ability of such a simple ecosystem model to be parameterised using easily accessible variables (e.g., breast heigh diameter and standing volume) makes it the appropriate tool. Nevertheless, further investigation is needed to reassure that the model is able to produce reliable results.

CHAPTER 7

A general discussion into the future of process-based models for sustainable forest management

7.1 Introduction

This thesis was developed with a unique strategic aim. The applicability of process-based models in a forest management context. Achieving such a huge objective is certainly something that demands a great effort in model development, calibration and continuing evaluation. It also requires the pressure of a forest management community willing to successfully substitute well established and easily implemented empirical growth models and yield tables. Finally, it demands the establishment of a long process of software development with simple and user-friendly GUI (Graphic User Interface), capable of providing the user with easy options for visualising and presenting the outputs of several management scenarios. Although such objective was out of the scope of this project, the specific objectives described in section 1.2 come from such a strategic planning. This thesis sets the basics elements for establishing process-based models within a framework of sustainable forest ecosystem production as a whole, while providing an adaptable tool for any specific management objectives. Undoubtedly, the scale of model development, calibration and testing and definition of exact classification procedures were limited due to limited time and resources. Nevertheless, the project could provide the necessary guidelines for a full scale, realistic program of continuous testing for several commercial species.

The study consisted of two major parts. The first was the development of a simplified

ecosystem process-based model, its calibration and testing for the study species, understanding the internal feedbacks of the model (Chapter 4) and applying the model to develop a classification framework for future forest management based on sustainability of ecosystem carbon production (Chapters 5 and 6). However, it is imperative for the successful development of such a site classification scheme that thorough knowledge of the growth of the species under study is available. The second part of the thesis, fulfils such a demand, by applying our knowledge of eco-physiological processes of Scots pine growth using an empirical (Chapter 3) and a process-based approach (Chapters 5 and 6).

7.1.1 Meeting thesis objectives

As it was set in Chapter 1 (page 2) the aim of the thesis was to develop a physiologically based model for forest management under a spatial framework. For that reason a set of nine specific objectives were set. Meeting those objective was a crucial part of this current work. More analytically:

1. The first objective was the development of a knowledge base for Scots pine across Scotland. The results of such a knowledge was presented in Chapter 3. The objective was met by using a multiple linear prinicipal component regression approach using a range of meteorological and productivity data collected from the field. Meeting the objective helped into developing a reference point of knowledge of the main climatic factors affecting Scots pine growth.

2. The second objective was the development of a new simple process-based model which introduces eco-physiological principles of forest production and soil decomposition. The objective was met by developing 3-PGN (Chapter 4) by integrating the simplified process-based models 3-PG and ICBM/2N.

3. Furthermore, the objective of calibrating, validating the model for Scots pine and exploring the uncertainty of model's parameters was met using the Bayesian calibration framework.

4. The investigation of the internal feedback was explored by conducting a sensitivity analysis (Chapter 4)

5. Running the spatial version of 3-PGN we were able to explore the physiological limitations on Scots pine growth and by using advanced spatial analysis techniques such as autocorrelation analysis we were able to explore the effect of environmental factors on Scots pine spatial patterns (Chapter 5).

6. Using the stand level mode of 3-PGN we were able to provide a discussion of which is the best management option, while we presented a methodology of how a new site classification procedure could be based on process-based model outputs (Chapter 6).

7.1.2 On the development of the simplified ecosystem model 3-PGN

For the study purposes, the process-based model 3-PGN was developed, by integrating one simple productivity model and one equally simple soil organic matter decomposition model. The linkage between the two models was achieved in such a way that the outputs of one became the inputs for the other. The logic behind such integration scheme was that the major processes occurring in forest ecosystems are linked by feedback loops with mutual interactions between above and below ground processes. Until know 3-PG has been a productivity model capable of predicting photosynthetic production and then transform it into biomass and timber using allometric relations and wood density, respectively. However, the lack of key soil processes such as organic matter decomposition, has made it impossible for users to represent ecosystem production. Additionally, the model was unable to ensure sustainability at the ecosystem level, as it did not provide any information about soil fluxes and pools. The linkage with ICBM/2N fills this gap using simple coupling between above- and belowground carbon production.

The soil sub-model was integrated with 3-PG to provide estimates of soil fertility, which was then employed in the routines of 3-PG. Obviously, simplification had to be introduced. For instance, nitrogen uptake from trees is a complex process involving

several biochemical reactions. Our approach has been to follow the original philosophy of 3-PG, i.e., to retain only a minimum level of complexity in the representation of the processes to avoid increasing the complexity of algorithmic modelling and the number of parameters. There was also the need to utilize existing algorithms from both models and at the same time to be based on well established theories of nutrient uptake. Landsberg (1986) provided the bases for establishing the newly modelled fertility rating. Based on the theory that under no limiting conditions, uptake would be proportional to the concentration of nutrients within structural tissues, we could estimate potential nutrient uptake for the stand as a whole. On the other hand, ICBM/2N with its existing nitrogen pools was able to establish an indication of potential mineral nitrogen availability into the soil. The ratio between them determined the fertility rating estimate.

The new fertility rating modelling removes the uncertainty associated with the estimation by the user following a soil survey and assumptions made according to soil texture and type. FR is not any more a direct indication of site fertility or a way to classify it. Now it is an internal parameter, which provides the necessary indication of the current nutritional status of the stand and how it will effect future production (a more appropriate term would be "fertility indicator"). Then comparisons among sites using this new FR may not be valid. However, the range of values take during a rotation and the time when this values occur may provide a comparison between sites. Although the need for manual adjustment of site fertility has now disappeared, we have introduced the uncertainty in the estimation of the new parameters. In addition, the number of parameters to be calibrated has increased. Despite this, the parameters needed can be very easily estimated by collecting of soil samples and estimating carbon and nitrogen stocks. In addition, we recommend that laboratory studies be conducted to determine the decomposition rates of the organic matter (i.e., in the litter and mineral soil) of the most important tree species.

Despite the successful linkage between the two models, certain pitfalls exist, which make necessary further testing and development of 3-PGN. Amongst the known pitfalls are first of all, the environmental effects on soil decomposition. Currently 3-PGN

introduces decomposition rates for the three pools, which are proportional to soil water availability and air temperature, following the basic assumption that decomposition takes place within a few centimetres of soil surface. Many Scots pine stands across Scotland are well established on very shallow soil, which makes such an assumption valid. However, this may introduce bias when it is applied to deeper soils (particularly against soils which tend to be more than usually insulated). The introduction of a soil temperature modifier should reduce the bias from such assumption. Such a modifier was not included in this project because of limited availability of soil temperature data. Future development should concentrate on establishing the depth that 3-PGN operates at and possibly introducing a depth-dependent soil temperature modifier.

A second pitfall of the project was the lack of availability of time-resolved data for soil carbon and nitrogen polls, to validate the estimates of soil carbon and nitrogen stocks. The availability of data for aboveground biomass simplified the calibration process and allowed to assume that model outputs were realistic for the chosen parameter set. The calibration procedure of 3-PGN was based on the Bayesian theorem, which provided the most likely values of the parameters given a specific calibration data set. Although the procedures of the Bayesian calibration produced reliable and trustworthy results, the availability of soil carbon and nitrogen chronosequence data set will reduce the uncertainty of the parameters (Van Oijen *et al.*, 2005). The calibration procedure followed in this study aimed to reduced this uncertainty by establishing multiple ”most likely” values for the key parameters including soil parameters, using published data from several sources and stands. An average of those values was assumed to be the most representative for the species. Although this is a time consuming but acceptable approach, future studies should concentrate into following a Bayesian calibration based on a time series data for C and N pools.

The temporal scale of the linkage between the two models is also a potentially serious pitfall, which could lead to biased results. Currently, 3-PGN operates with a monthly time step, while ICBM/2N was designed to operate annually. Time steps however, were levelled for the study by assuming that current soil algorithms can be employed at the lower temporal scale. This was necessary to obtain a better under-

standing of the internal feedbacks between the two models. This means that changes in soil fertility occurred in a monthly step, which can lead to extreme monthly values and extreme monthly predictions of carbon production. Over a long simulation period (e.g., 100 years), such an effect is moderated by the repeated overestimations and underestimations, however this could be problematic when shorter simulation periods are employed. Furthermore, the lack of soil carbon and nitrogen data did not allow the verification that the current temporal scale produced reliable results. Future development should consider establishing different time steps over which soil processes and stand development are simulated, while testing against a soil data base.

3-PGN also introduces another assumption which comes with the adoption of the new fertility rating. Nitrogen uptake currently depends on leaf nitrogen concentration, which was considered the most nitrogen demanding tissue. However, more reliable results may be obtained if include other tissues, such as roots and stems, were also included, to vary whole plant nitrogen demand between species. Additionally, previous studies (Running and Gower, 1991) showed that nitrogen concentration varies with leaf area index, allowing adjustment of nitrogen concentration over time and, most importantly, over space. Although temporal changes of nitrogen concentration were considered negligible, further investigation into this assumption is necessary.

Finally there has been a discussion into the validity of the thinning algorithms of 3-PG. Currently, thinning is based on the fraction of foliage, stem and root biomass of a single tree removed by the thinning. According to Sands (2004), 3-PG does not respond correctly to thinning or defoliation, as it cannot produce closure of canopy because partitioning is based on average stem diameter. Further research should be encouraged into developing more process-based algorithms of biomass allocation which will allow not only response of biomass allocation to silvicultural events but also to natural hazards such as wind and fire.

7.1.3 On Bayesian calibration

The Bayesian approach to calibration combines a priori expert judgement with sampling information (data) to produce a robust posteriori model. However there are several consideration for its use, which one needs to consider to avoid reaching the wrong conclusions. First is the prior distribution. When no information are available for the prior distribution of the parameters, then it is most sensible to assume a uniform distribution with a lower and an upper limit. A comprehensive literature review can provide an indication of those limits although that may prove very difficult when applying the model to a certain species for the first time. Although limits can be set based on the current knowledge of the modeller, an extensive field measurement campaign will ensure the development of a prior knowledge and will certainly improve the quality of the ”most likely” parameter vector, by significantly reducing uncertainty in their prediction. On the other hand, this is a technique applicable even with a small dataset and can provide a general knowledge of the parameters and outputs uncertainty, which is normally impossible with a manual calibration. Also an automated method such as this, is certainly more efficient into choosing parameters for models with a large parameter vector. However, it does not provide the user with an ”optimum fit”. A calibration strategy, where several Bayesian calibrations are applied for a number of sites across a region, can provide a mean parameter vector applicable to all regions. Future applications of 3-PGN should consider combining Bayesian calibration based on data obtained from an established network of sample plots.

7.1.4 On Scots pine productivity

Productivity of Scots pine varies greatly because of its wide distribution across environments (see distribution in Section 1.3). In Scotland, where it is native, natural Scots pine woodlands are mostly characterised by very low levels of productivity. On the other hand, plantation of Scots pine can vary significantly in productivity across Scotland due to the dramatic changes in the climate between the East - West and the North - South axes (Chapters 3 and 5). Understanding and identifying the major effects of

climate on growth was a central part of the thesis. Chapters 3 and 5 provide an investigation using both empirical and process-based approaches. The general conclusion was that Scots pine growth is significantly restricted by low winter temperature and the possibility of growth restriction due to frost is more likely, while lack of precipitation also seems to have an negative effect (Chapters 3 and 5) due to a significant drought effect occurring during early spring-late summer. Finally, it was found that Scots pine has the potential to photosynthesise during winter months when temperatures are not significantly low, while ammonium is the mineral form of nitrogen that has an affect on growth.

7.1.5 On GIS and spatial analyses

GIS is a very powerful visualisation tool, but it is also much more than an advanced mapping tool. It can also be a very powerful analysis tool, providing a series of spatial analyses capabilities based either on vector or raster data format, including geostatistics, network analysis, buffering, map algebra, cluster analysis, regression and principal component analysis. These advanced capabilities however are frequently not fully explored by forest scientists into their exploration of natural processes and of their spatial distribution. Except for a few exceptions, the utilisation of GIS most of the time is limited to visual interpretation of results, or producing outputs from statistical regression models using digital elevation models as one of their independent variables. This study attempted to utilise advanced spatial analysis techniques based on raster-type of data in order to obtain a better understanding of the underlying eco-physiological processes affecting Scots pine growth. The produced spatial outputs were analysed using a series of advanced techniques such as spatial principal component regression analysis, correlation and autocorrelation analysis which gave an understanding of why the observed spatial patterns occur. Apart from the visualisation of the outputs, GIS provided the platform for investigating the temporal and spatial changes of Scots pine productivity and identified the main climatic and topographic effects responsible for the observed spatial patterns, using an autocorrelation analysis to infer spatial clustering. Amongst the aims of this study was to demonstrate and encourage the application of such ad-

vanced spatial analysis techniques in forest science.

7.1.6 On Ecological Site Classification

ESC is an application capable to provide an indication of soil fertility and moisture based on association of nutrients with a series of soil properties, such as soil texture, rooting depth and stoniness, as well as associations with many indicator plant species. Additionally, ESC provides an indication of species suitability and a prediction of potential yield class. Finally, it provides an identification of the most important limiting factor for growth. Although it can be a very useful tool some limitation were illustrated from this study (Chapter 3). It appears that ESC was unable to capture some of the important limiting factors for growth such as lack of precipitation and limited photosynthesis during winter. Yield predictions on the other hand, were significantly different from field observations but not from model predictions (Chapter 5). Although the validity of the soil nutrient and moisture predictions of ESC were not directly questioned, they appeared to be reliable (see PCA results in Chapter 3). Further research however, is necessary for improving how environment limits growth. A way forward, would be the possible integration of ESC with 3-PGN, where the first will provide information about nutrient and carbon for 3-PGN, whereas the latter will include a physiologically based limitation on growth and a prediction of potential yield class.

7.2 A novel strategy for British forestry

Similar to other European and international agencies, British forestry agencies are embracing application of modern technologies for forest management and research. The continuing efforts for establishing an organisation scheme has evolved into a unique decision support system (DSS) network, based on an extensive forest database, also known as FORESTER, fully integrated under a GIS framework and more recently under a web-based GIS framework. Nowadays, managers in any forest district of the country can access forest mensuration data and visualise the output. In addition, several other DSS developed by Forest Research (such as ESC and ForestGALES) are

available to all managers to support decisions based on site-specific knowledge (ESC) or on assessment of the risk of wind impact (ForestGALES). The current strategy includes the integration of all independent DSS within the current spatial framework of FORESTER. But where does process-based modelling fit within this current strategic planning?

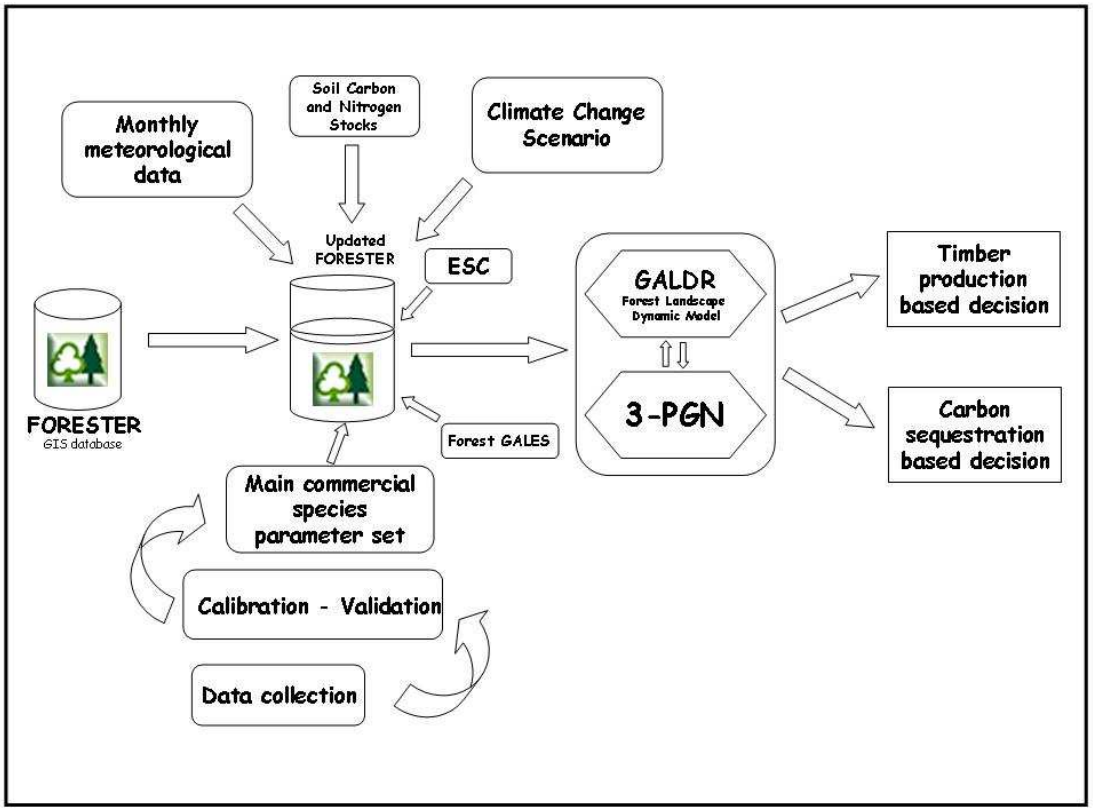

Figure 7.1: A novel strategy for the future of forest management based on the full integration of process-based models under a GIS framework for multiple purpose decision making.

Although recently Forest Research has embraced process-based modelling by development of the ForestGROWTH, a physiological process model for growth and ForestETP a complex model of water transport, little has become part of an applicable tool. A realistic answer to the above question can come with the introduction of a novel strategy, which tries to establish the vision under which a simplified process-based model such as 3-PGN could be successfully used for forest management of British forests. Figure 7.1 illustrates the six steps of this strategy.

7.2.1 Calibration - Validation

The first step includes the collection of the necessary time-resolved datasets that will provide the bases for calibration and validation of the model for all the main commercial species. Datasets such as above and belowground biomass, net ecosystem production and soil carbon and nitrogen stocks and fluxes could come from a well established network of permanent sample plots across the country for several commercial species. Eddy covariance measurements can also provide the necessary quality data for model calibration.

A calibration procedure based on Bayesian approach, similar to the one presented in Chapter 4 will be able to incorporate site variability and parameter uncertainty by producing a unique parameter vector, while a database of posterior distributions could provide the prior knowledge of future calibration procedures. Calibration procedures such as the one followed in this study will reduce the number of parameters for which site-specific calibration is required and consequently the potential for biases in their estimates. The strategic planning could potentially include the periodic (e.g., after five years) re-calibration of the most uncertain and most significant parameters of the model, by utilizing existing prior knowledge and new data collected from the network of permanent sample plots. This will ensure that forest productivity modelling retains its validity vis-a-vis any potential environmental changes that have a significant impact on a tree growth (e.g., extensive droughts). Validation of the parameter set will be based on an independent national dataset which will provide the necessary reassurance that the produced parameter vector gives reliable results.

7.2.2 Meteorological data - Climate change scenario

The next step include the collection of the meteorological data necessary for the model. Currently a well established network of meteorological stations exists throughout the country. Collection of maximum and minimum temperature, precipitation and incoming solar radiation could provide the dataset which 3-PGN will utilize for predictions. This dataset could be either in point mode, for specific areas which users will be able to

query, or on a spatial mode if necessary. Interpolation of climatic variables using geostatistics is a common practice, capable of providing not only predictions of spatially interpolated values but also an estimate of the error introduced in the prediction. Additionally, several climatic scenarios produced by the Met Office could be also available for future prediction of the effect of forest ecosystem productivity. Periodic updates (e.g. five years) of the climatic database will ensure that any climate change does not remain only as scenarios but is also introduced into model predictions.

7.2.3 Soil data

Soil data are one vital part of 3-PGN in order to provide the possibility of a reliable estimates of ecosystem production. Necessary soil data should be included in a database from an extensive network of permanent sample plots. Nitrogen availability, soil organic matter decomposition rates and carbon stocks (divided by the major pools), soil texture and available soil water content are amongst the necessary inputs of the model, which field data should be capable to provide. Additionally, when necessary spatial data should be also available. As interpolation of soil data could be extremely uncertain due to high spatial variability, information about soil nutritional status and carbon stocks could be derived through associations of a combination of variables such as soil type, texture, ground species etc. Currently ESC provides such indication of soil nutrient and moisture but with a descriptive and summarized way. Further research however and a modification of the existing ESC knowledge base could provide estimates on stand, regional or national scale.

7.2.4 Sustainable ecosystem production

The new strategy should not however reject any current forest management theories. The principles of sustainable forest yield production have been applied to forest management for a long time. In addition, the new continuous-cover forestry approach of British forestry demands a better understanding and application of the theory and its enlargement to include aspects of sustainability that go beyond forest yield. Normality

of forest yield was achieved through a constant timber production, while sustainability of forest production is ensured by predicting the sustainable yield using Equation 7.1:

$$E = Z + \frac{V_C - V_N}{a} \tag{7.1}$$

where E is the annual sustainable yield, Z is volume increment, V_C current stock of stand volume, V_N normal stock of volume, a period required for equality between V_C and V_N.

However, carbon sequestration and the role of forest in mitigating climate change are becoming more and more important in shaping management policy. Therefore sustainability of forest production should be established at the ecosystem production scale and not only for timber production. Normal carbon production tables could be constructed, as demonstrated in Chapter 6 using 3-PGN outputs, to explore the variability of a species production across the country. The tables should be based on the accumulation of net ecosystem production. To ensure sustainability of forest ecosystem production, the above equation should be modified as:

$$E_C = P_E + \frac{S_{E_C} - S_{E_N}}{a} \tag{7.2}$$

where E_C is the annual sustainable carbon yield, P_E is the net ecosystem production or carbon increment, S_{E_C} current stock of ecosystem carbon, S_{E_N} normal stock of ecosystem carbon, a period required for equality between S_{E_C} and S_{E_N}. Normal carbon tables should be also capable of providing estimates of timber increment and stocks.

With Equation 7.2 it would be possible to ensure carbon removal from a forest ecosystem, while maintaining carbon stocks. However, ensuring sustainability on ecosystem level bring on the surface one very important question. Should sustainability be ensured before or after the losses of carbon through respiration were accounted. If sustainable carbon yield is estimated before respiratory losses then in Equation 7.2 P_E

should be substituted with P_G. In such a case carbon yield will include both respiratory losses and actual carbon removed from the ecosystem. But what would be the effect on actual carbon stocks as carbon yield becomes highly sensitive to climatic conditions, with warmer climate increasing respiration and reducing carbon removed. On the other hand, when sustainable yield is estimated after respiration losses then it directly represents direct carbon removals but with the question of the impact on carbon stocks still valid. Thus, further investigation into the impact of such a strategy on carbon sequestration is absolutely vital.

Normal yield tables should not be totally rejected. On the contrast, whenever timber production is the principal objective of the forest management, then revised yield tables (with a revision strategy as demonstrated in Chapter 6) should be able to describe the normality in terms of timber production. Additionally, normal yield tables should be also capable to produce carbon production estimates so as to provide information of how much carbon is sequestered. It should not be assumed that stands characterised by high yield are also characterised by high levels of carbon sequestration.

Knowing which stands should follow a carbon sequestration or a timber production management objective is vital to determine which normality objective should be targeted. An investigation using 3-PGN (Chapter 6) should be conducted to identify stands most suitable for one or the other objective. In the study case of Scots pine for example, currently low yield class stands were found to be more significant for carbon sequestration and so normality in carbon production should be ensured by arranging appropriate silvicultural treatments.

However, identifying suitable stands demands a site classification scheme capable of identifying suitable for either carbon sequestration or timber production. Chapter 5 demonstrates such a classification scheme based on 3-PGN SPATIAL, identify areas where potentially Scots pine could maximize carbon accumulation. After identification managers should be capable of deciding which management option to follow.

7.2.5 3-PGN and stand dynamics

A strategy derived based on a continuous-cover forestry approach demands a model capable of estimating not only ecosystem carbon production but also stand dynamics. To incorporated the possible effect of either human or natural disturbances on the dynamics of an uneven-aged stands demands a model having such capabilities.

Recently, authors have linked process-based productivity models and gap models, particularly Seidl *et al*. (2005), who integrated 3-PG with the gap model PICUS and Zuo *et al*. (2003), who linked 3-PG with the gap model GROWEST. So far 3-PG has been applied only to even-aged, single-species plantations. In several countries however, forest management is concentrating into continuous cover forestry to fulfil multi-purpose management including timber production, recreation and tourism, protection from soil erosion and atmospheric carbon sequestration. Thus, it is vital to develop and complete 3-PGN for continuous cover forestry, by removing the current algorithms of stem thinning and by introducing an equally simplistic gap type model, to provide the ecological base modelling for succession, regeneration and natural mortality. Additionally, such a model should include the effects of wind or fire into the ecology of the forest ecosystem. A characteristic example of such a model is GALDR (Hope *et al*., 2006), a landscape dynamics model capable of simulating natural disturbance and succession. GALDR utilizes information about species composition, stocking density and age structure, while using environmental factors derived from ESC (Pyatt *et al*., 2001). A direct linkage with 3-PGN would provide GALDR with an estimation of photosynthesis and of the environmental effects on growth, while GALDR would predict the effect of competition and natural hazards on stand density. Furthermore, GALDR would provide an estimate of the brash left out after residuals silvicultural practices or natural disasters, which return organic matter into soil carbon.

7.2.6 Database integration with FORESTER

The final step of this novel strategy includes the integration of all the above with the current spatial framework of FORESTER. Individually developed databases of for-

est growth, meteorological data, soil survey data and parameter sets for major commercial species could become one unique central dataset accessible through a web-based design. ESC and ForestGALES come to complete the integrated and updated FORESTER database providing data and algorithms necessary not only for decision making but also as inputs for the newly coupled uneven-aged, fully ecosystem and simplistic productivity process-based model 3-PGN-GALDR.

Managers should be able to have a locally installed updated version of the productivity model under either a locally installed and customised GIS software (e.g. ArcGIS) or more conveniently under a web-based GIS. Before management decisions are taken, the manager will be able to run the productivity model using input data from the central FORESTER database, either on a spatial or point mode. Model simulation outputs should then been able to be reported in an easy, understandable, spread-sheet style format. The manager will also be able to conduct a site classification based on the spatial model outputs which could help supporting planting decisions. Normal predictions for the species under study should be also available through the central FORESTER database and automatically retrieved and compared with either model estimates of current production or future scenarios. The sustainable ”yield” then is estimated. The manager should also be capable of accessing several climate, wind or silvicultural scenarios, and produce model results which then could be compared. By estimating the sustainable ”yield” of different scenarios, the manager should be able to reach a decision depending on the management objective of the forest as well as necessary operations and actions. Finally, the manager should be able to integrate the output decisions into a mapping tool provided by the GIS application by accessing spatial datasets of roads, vegetation and soil information, producing maps including future estimates of carbon sequestration based on model outputs.

7.2.7 Spatial scale and data consideration

One major consideration of the strategy is the chosen spatial scale and the data necessary. Model results should be produced both in a point and in spatial context. When point mode is used, results would be presented in a per hectare basis and all decision

should be based on that. However, when there is a necessity for visualising productivity and its spatial variations, then spatial simulations should produced. Data by the central database should be spatially interpolated, as 3-PGN requires many inputs whose spatial variability should be included. When it comes to strategic, national scale planning, it would be straightforward to develop a single spatial dataset of inputs for the whole country with a large spatial resolution (e.g., 5 km or 10 km). However, when it comes to regional and local simulations then data must have a finer spatial resolution (e.g., for 1 km to 50 m), with an extent matching that of a forest district. This need for localised spatial data may prove to be the weakest point,given the economical and technical challenges in obtaining such data.

In this case, decentralisation of the data collection responsibilities is necessary. Forest district should be able to establish and maintain a network of permanent sample plots which will provide the necessary data. Processing of the data and interpolation could be then either forwarded into a central department or could be either locally produced by specialist, although the second option could be proven not so straight forward. Then produced localised spatial inputs should be entered in the database and be available not only to the districts managers but to all registered users.

7.3 Final remarks - future research and development

With regard to process-based models, there are two directions that should be explored. Firstly, the introduction of routines capable of predicting regeneration of woodlands based on current environmental and soil conditions, and secondly the integration of the whole package into a web-based GIS framework. When remote sensing comes also into alliance, then the result is a more powerful tool for sustainable forest management decisions. The future framework of any national forest service should be the introduction of a GIS web-based tool utilizing spatially extended climatic and soil with remotely sensed inputs of leaf area index, providing simulations with process-based models and creating a database of potential scenarios based on management decisions. Model predictions should include both timber and carbon based predictions, which

later should be capable for visualisation through a web-based GIS version freely available to all managers for decision making.

With regard to research, developing an ecosystem model capable of simulating carbon balance of uneven-aged stands could be a very useful tool into answering questions such as what are the respiratory losses during and after timber extraction operations, how much carbon is removed during yield removal operations, which silvicultural system is more vital for achieving carbon sequestrations and what is the likely impact of current forest operation and climate change on ecosystem carbon dynamics between uneven-aged and plantation forests.

This thesis aimed to close the gap between tree physiological research and forest management practice by using models to established new methodologies of decision making. At the same time, it contributes to forest science by providing a detailed ecophysiological interpretation of the environmental factors affecting Scots pine growth, a species with great variation in its European distribution. Setting a strategic framework and developing the tools for sustainable management of the worlds forests is the only way to ensure there is continued existence in the face of the present and future challenges.

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APPENDIX A

Productivity maps

This part of the appendix presents 3-PGN SPATIAL spatial predictions for the patterns of:

- Net ecosystem production (P_E, $\mathrm{tC\ ha^{-1}\ yr^{-1}}$, Figure A.1, Page 280)
- Net primary production (P_N, $\mathrm{tC\ ha^{-1}\ yr^{-1}}$, Figure A.2, Page 282)
- Ecosystem respiration (R_E, $\mathrm{tC\ ha^{-1}\ yr^{-1}}$, Figure A.3, Page 284)
- Stand volume (V, $\mathrm{m^3\ ha^{-1}}$, Figure A.4, Page 286)
- Mean annual increment (MAI, $\mathrm{m^3\ ha^{-1}\ yr^{-1}}$, Figure A.5, Page 288)

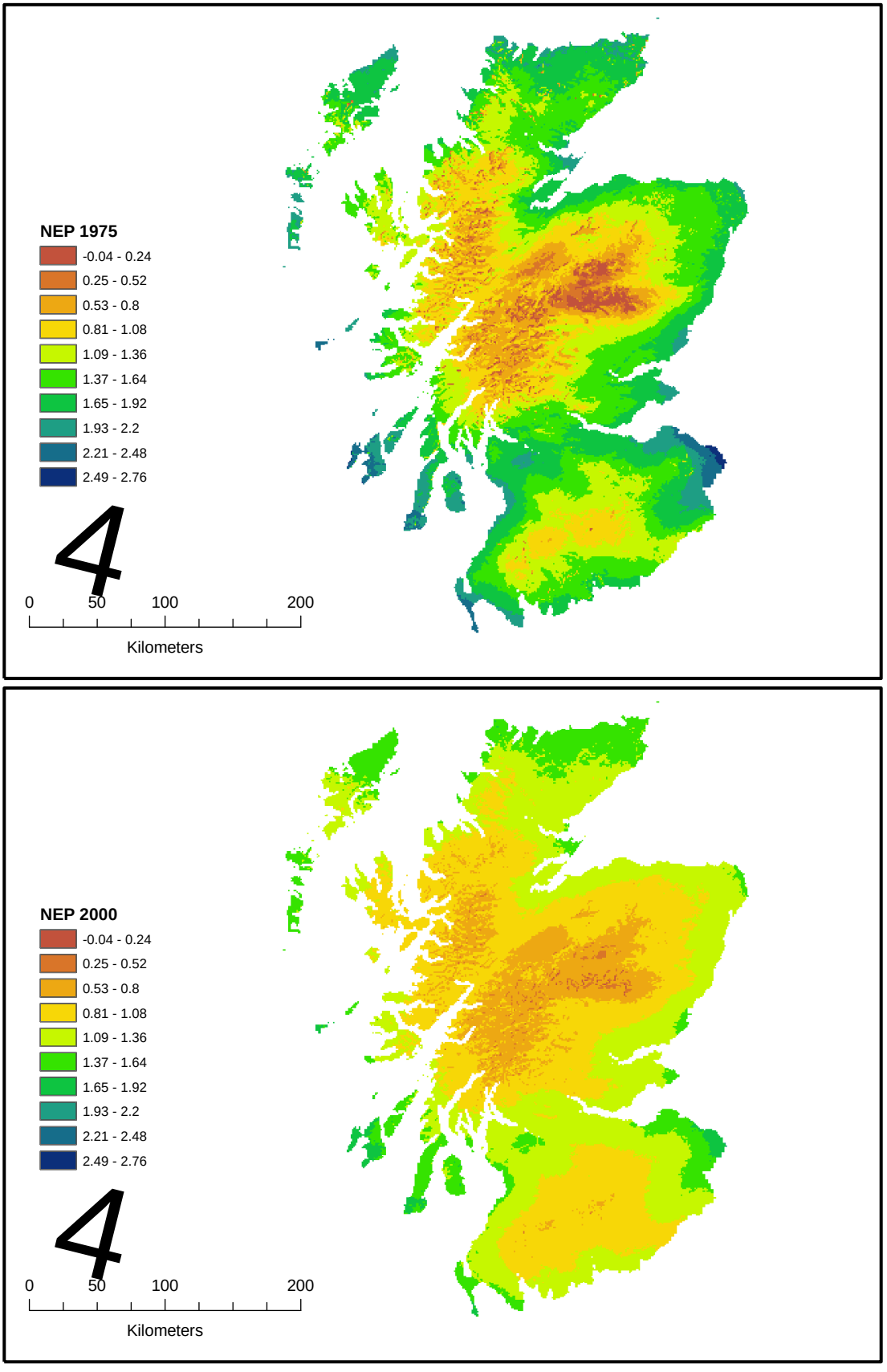

Figure A.1: Temporal changes of net ecosystem production (P_E, $\mathrm{tC\,ha^{-1}\,yr^{-1}}$) spatial patterns as they were predicted by 3-PGN SPATIAL.

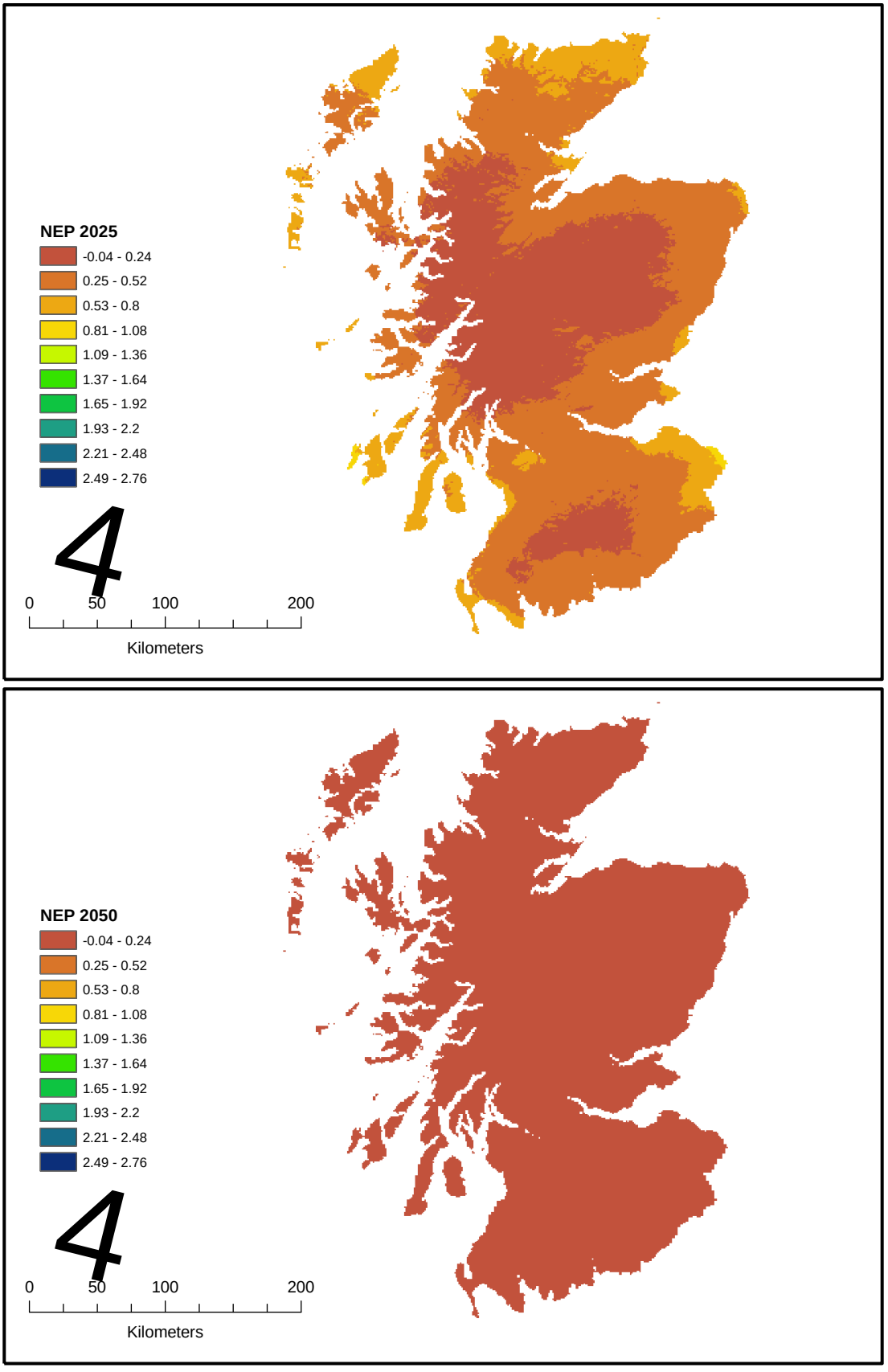

Figure A.1: *Continued*

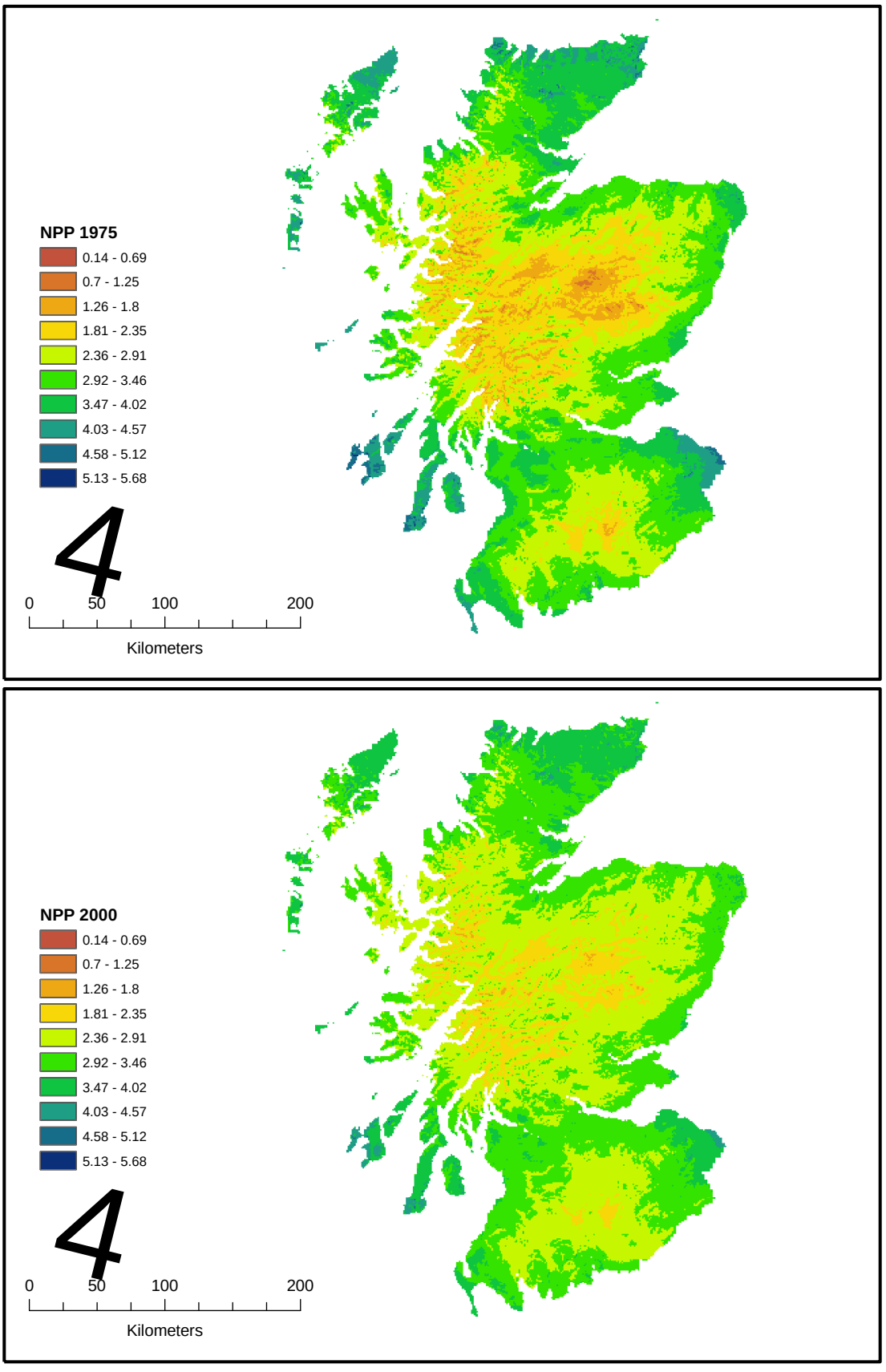

Figure A.2: Temporal changes of net primary production (P_N, $\mathrm{tC\ ha^{-1}\ yr^{-1}}$) spatial patterns as they were predicted by 3-PGN SPATIAL.

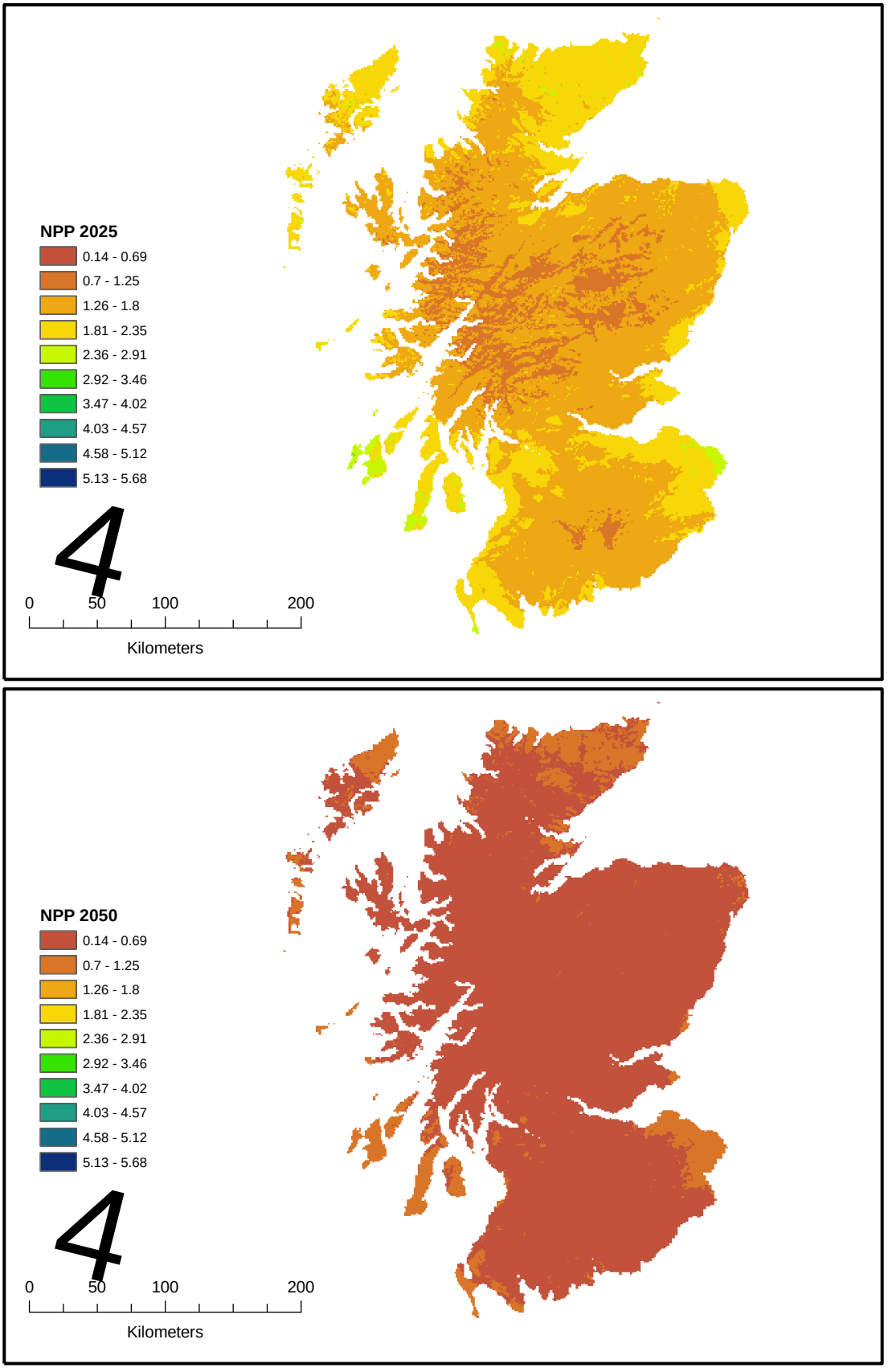

Figure A.2: *Continued*

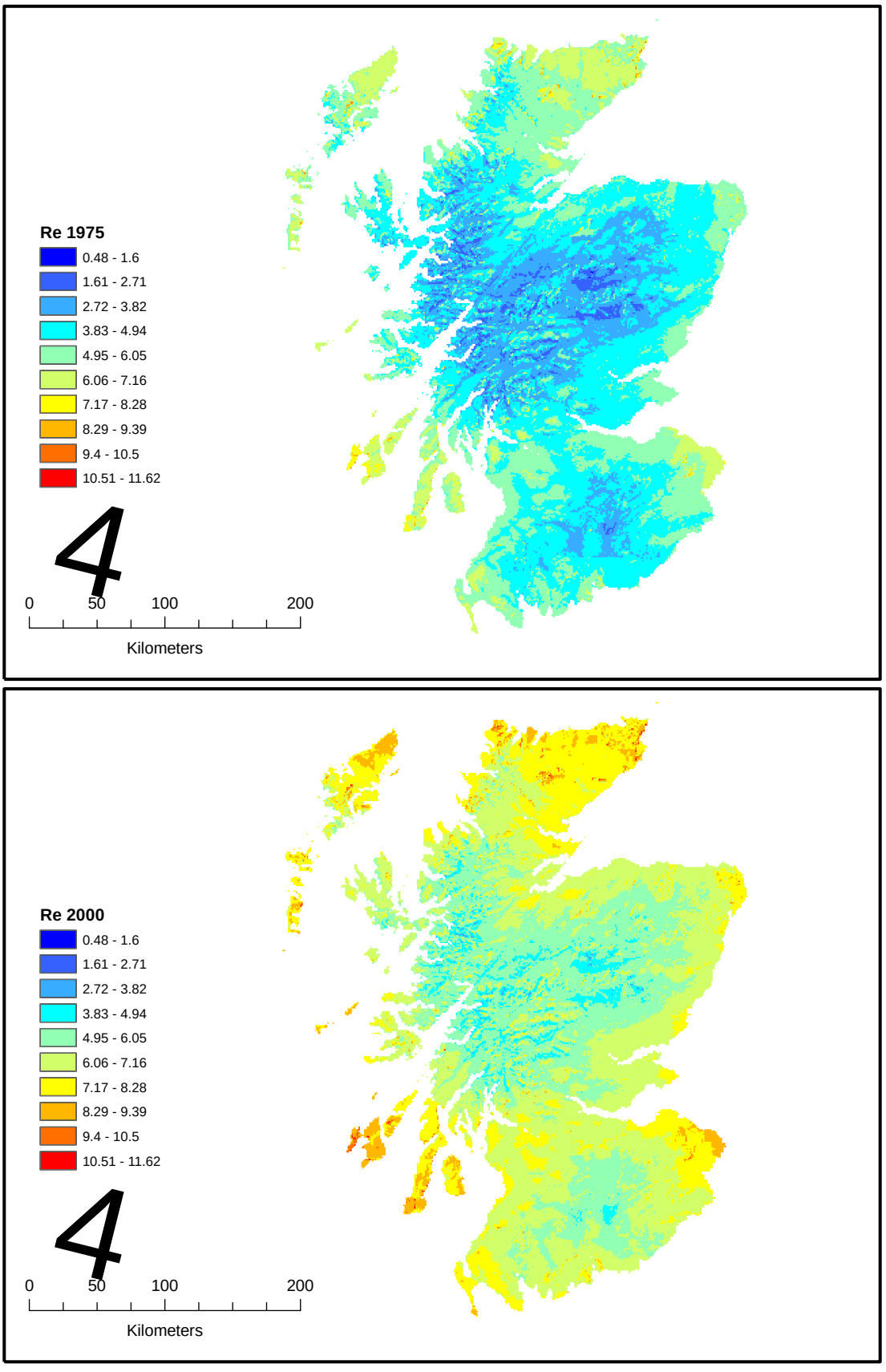

Figure A.3: Temporal changes of ecosystem respiration (R_E, tC ha^{-1} yr^{-1}) spatial patterns as they were predicted by 3-PGN SPATIAL.

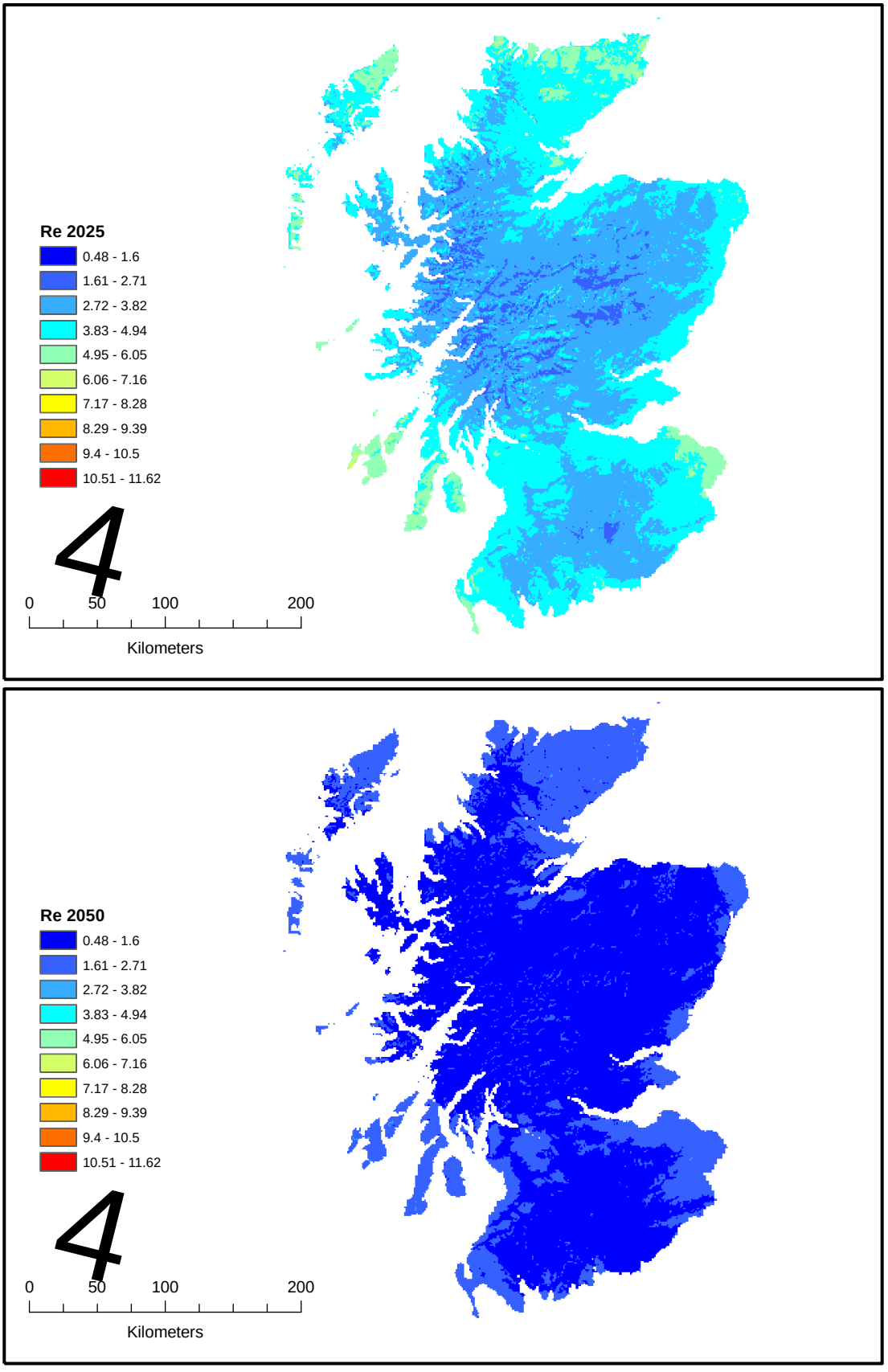

Figure A.3: *Continued*

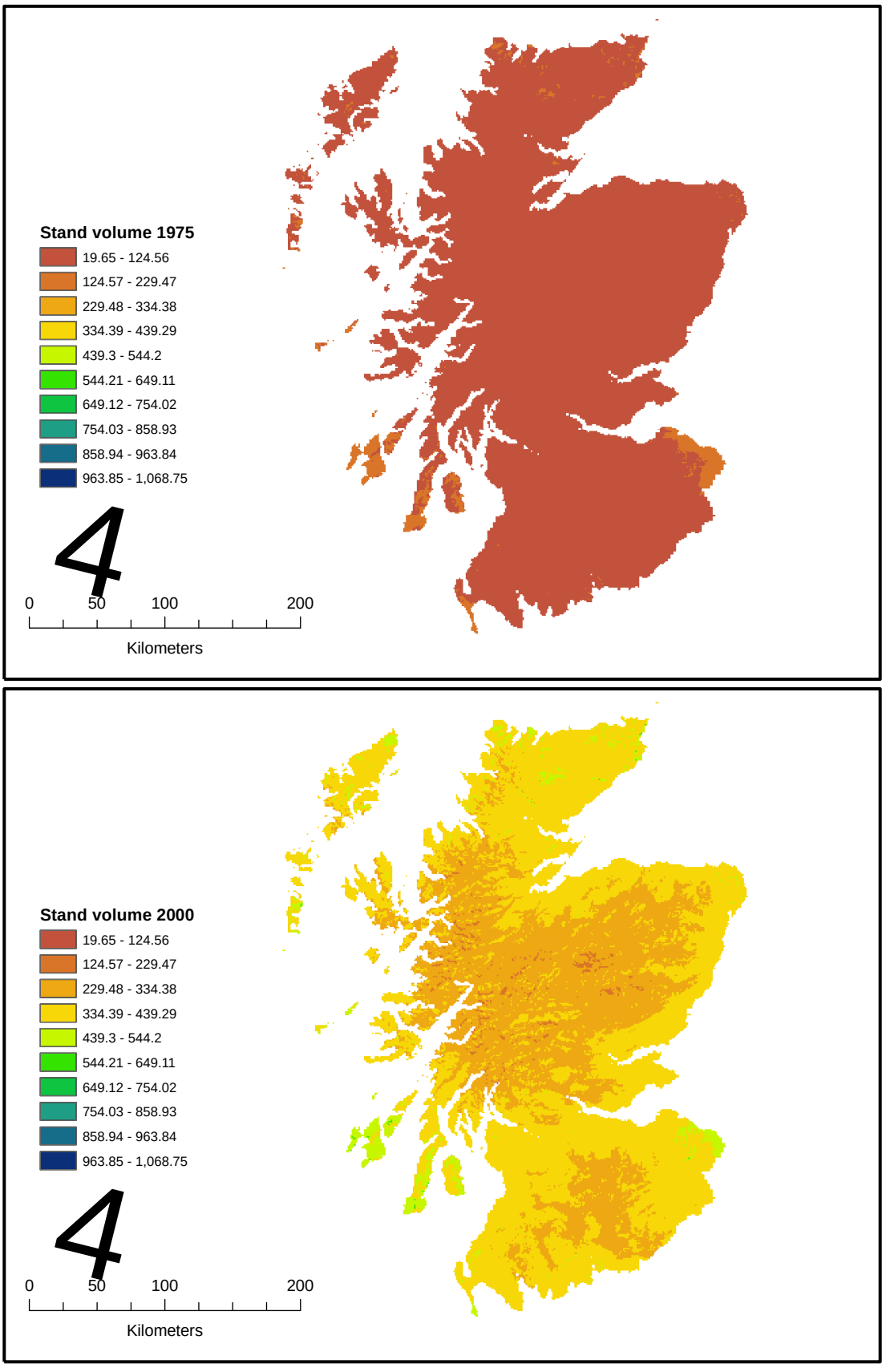

Figure A.4: Temporal changes of stand volume (V, $\mathrm{m}^3\,\mathrm{ha}^{-1}$) spatial patterns as they were predicted by 3-PGN SPATIAL.

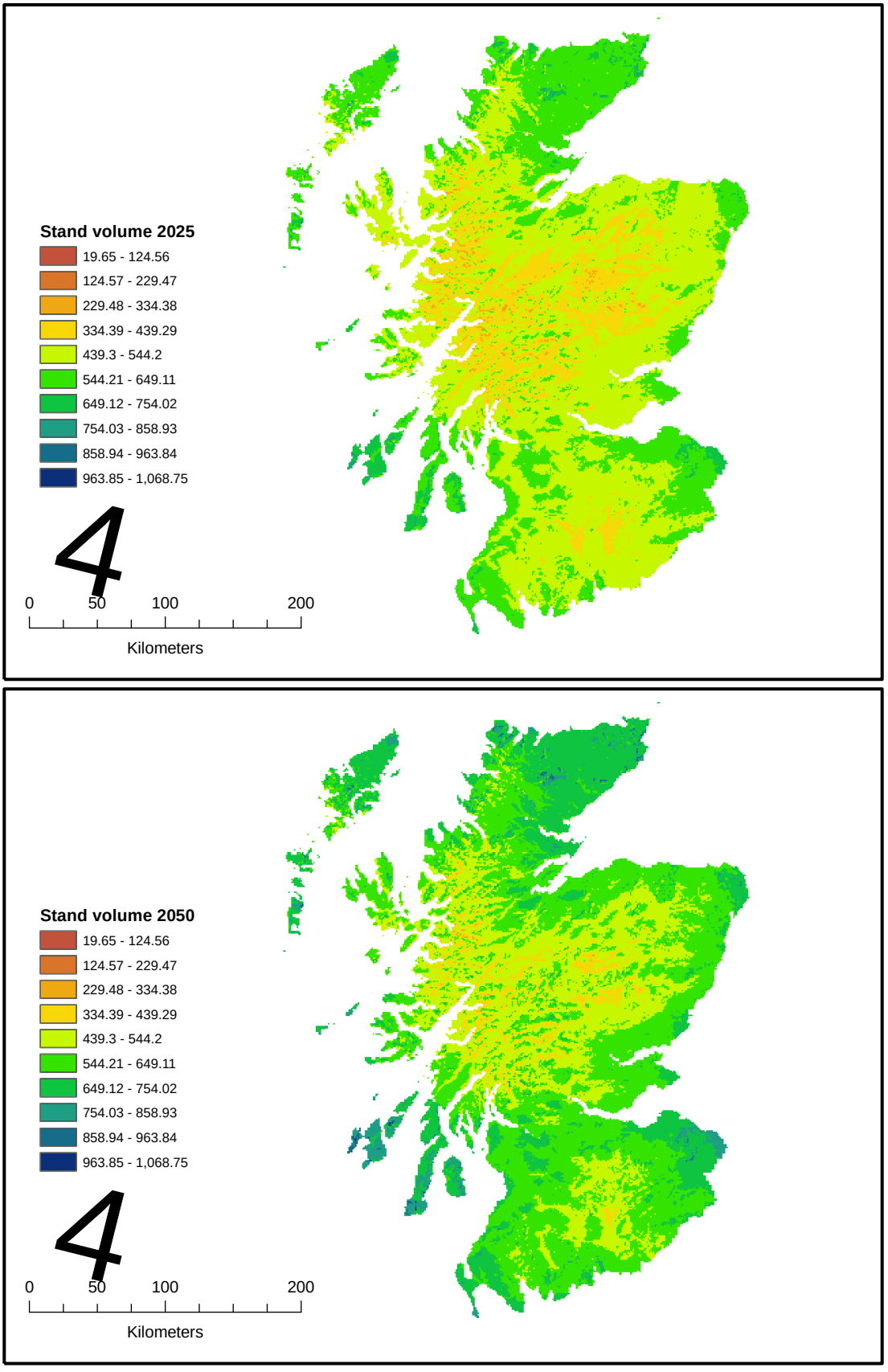

Figure A.4: *Continued*

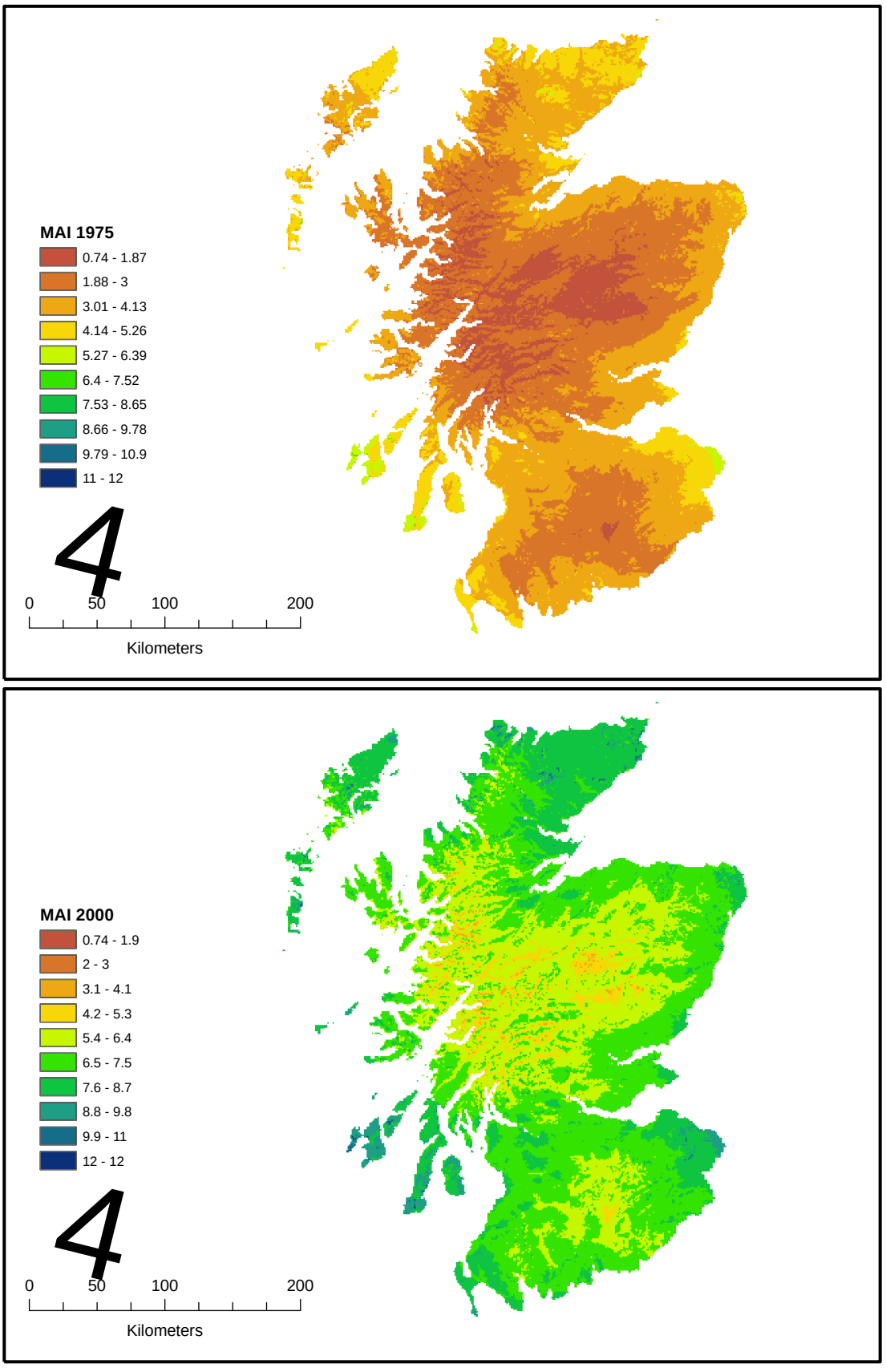

Figure A.5: Temporal changes of mean annual volume increment (MAI, $\mathrm{m}^3\ \mathrm{ha}^{-1}\ \mathrm{yr}^{-1}$) spatial patterns as they were predicted by 3-PGN SPATIAL.

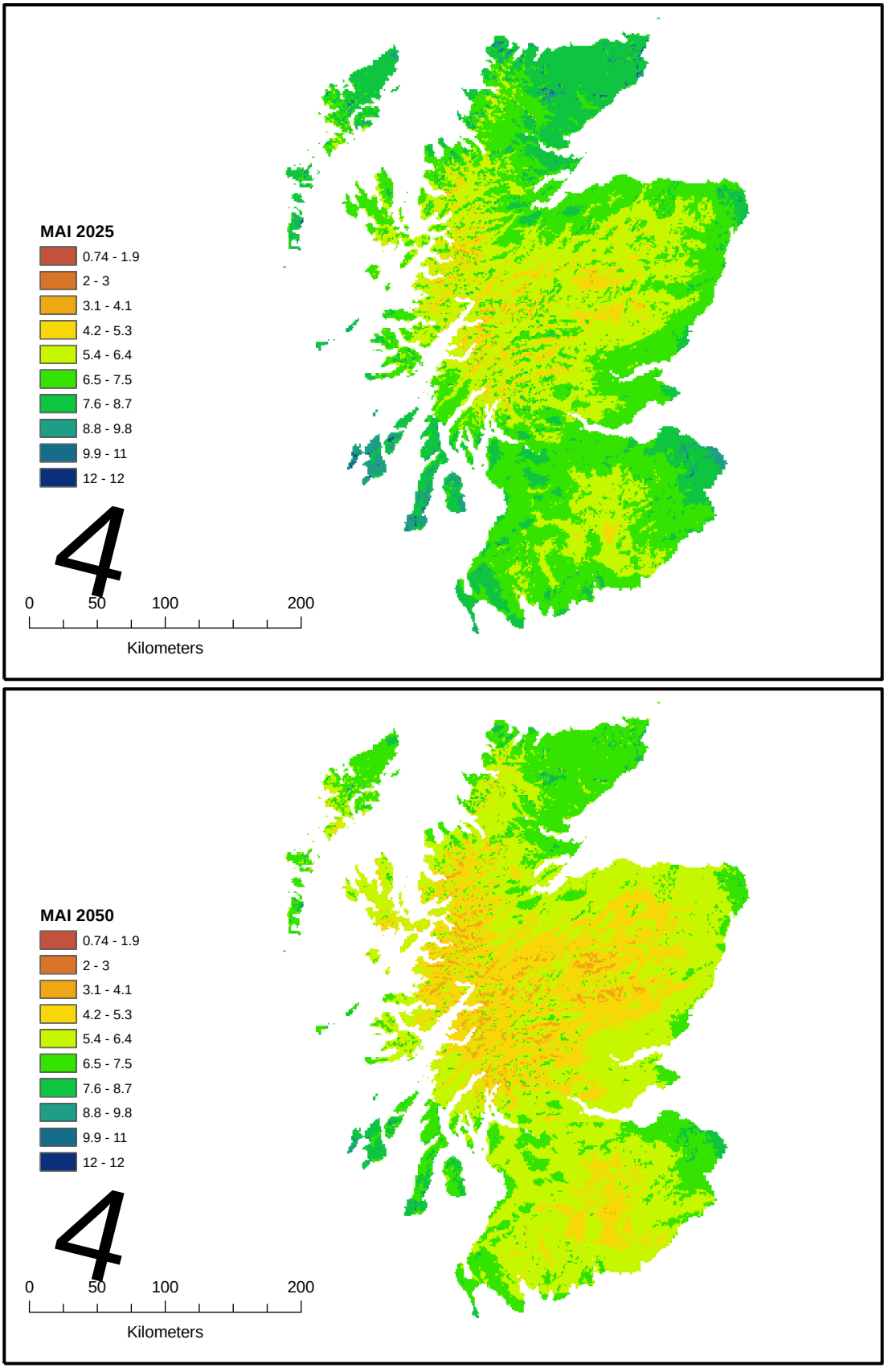

Figure A.5: *Continued*